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CONTENTS

	PAGE
BREESE, M. H.	
The infestibility of stored paddy by <i>Sitophilus sasakii</i> (Tak.) and <i>Rhyzopertha dominica</i> (F.) (illustrated)	599
BROWN, A. W. A., MCKINLEY, D. J., BEDFORD, H. W. & QUTUBUDDIN, M.	
Insecticidal operations against Chironomid midges along the Blue Nile (illustrated)	789
BROWNE, S. G.	
Observations on <i>Simulium neavei</i> Roubaud, with special reference to a focus of onchocerciasis in the Belgian Congo (illustrated) ...	9
BURGES, H. D.	
A spear for sampling bulk grain by suction (illustrated)	1
BURGES, H. D.	
The effect of temperature, humidity and quantity of food on the development and diapause of <i>Trogoderma parabile</i> Beal (illustrated)	685
BURSELL, E.	
The measurement of size in tsetse flies (<i>Glossina</i>) (illustrated) ...	33
BURSELL, E.	
The effect of humidity and temperature on the extent of abdominal pigmentation in <i>Glossina pallidipes</i> Austen (illustrated) ...	39
BURSELL, E.	
The effect of temperature on the consumption of fat during pupal development in <i>Glossina</i> (illustrated)	583
BURSELL, E. & GLASGOW, J. P.	
Further observations on lake-side and riverine communities of <i>Glossina palpalis fuscipes</i> Newstead (illustrated)	47
CHAPMAN, R. F.	
A note on <i>Glossina medicorum</i> Aust. (Diptera) in Ghana (illustrated)	435
CORNWELL, P. B.	
Movements of the vectors of virus diseases of cacao in Ghana. II.—Wind movements and aerial dispersal (illustrated)	175
CRANHAM, J. E.	
Insect infestation of stored raw cocoa in Ghana (illustrated) ...	203
LA CROIX, E. A. S.	
A trial use of grass-mat passages in protecting humans from attacks by tsetse flies	639
DAS, G. M.	
Occurrence of the red spider, <i>Oligonychus coffeae</i> (Nietner), on tea in north-east India in relation to pruning and defoliation ...	415
DAVIES, H. & BLASDALE, P.	
The eradication of <i>Glossina morsitans submorsitans</i> Newst. and <i>Glossina tachinoides</i> Westw. in part of a river flood plain in Northern Nigeria by chemical means. Part III (illustrated) ...	265

DE LOTTO, G.	
The green scales of coffee in Africa south of the Sahara (Homoptera, Coccidae) (illustrated)	389
DOBSON, R. M. & MORRIS, M. G.	
Observations on emergence and life-span of wheat bulb fly, <i>Leptohylemyia coarctata</i> (Fall.), under field-cage conditions (illustrated)	803
DUNN, J. A.	
The natural enemies of the lettuce root aphid, <i>Pemphigus bursarius</i> (L.)	271
DUTT, N.	
Studies on the bionomics of the jute stem girdler, <i>Nupserha bicolor postbrunnea</i> Dutt (Col., Lamiidae) (illustrated)	765
EADY, R. D.	
<i>Pentalitomastix</i> , a new name for <i>Pseudolitomastix</i> Eady (Hymenoptera, Chalcidoidea)	173
FERNANDO, H. E.	
A biological and ecological study of the rice Pentatomid bug, <i>Scotinophara lurida</i> (Burm.) (illustrated)	559
GEERING, Q. A. & COAKER, T. H.	
The effects of different plant foods on the fecundity, fertility and development of a cotton stainer, <i>Dysdercus supersticiosus</i> (F.) (illustrated)	61
GILLIES, M. T. & SMITH, A.	
The effect of a residual house-spraying campaign in East Africa on species balance in the <i>Anopheles funestus</i> group. The replacement of <i>A. funestus</i> Giles by <i>A. rivulorum</i> Leeson (illustrated)	243
GLASGOW, J. P.	
The variability of fly-round catches in field studies of <i>Glossina</i> (illustrated)	781
GLASGOW, J. P. & BURSSELL, E.	
Seasonal variations in the fat content and size of <i>Glossina swynnertoni</i> Austen (illustrated)	705
GOMA, L. K. H.	
The swamp-breeding mosquitos of Uganda: records of larvae and their habitats	77
GOSTICK, K. G. & HEWLETT, P. S.	
Killing house-flies, <i>Musca domestica</i> L., by means of hanging drops of insecticide (illustrated)	523
GRIFFITHS, D. C.	
The behaviour and specificity of <i>Monoctonus paludum</i> Marshall (Hym., Braconidae), a parasite of <i>Nasonovia ribis-nigri</i> (Mosley) on lettuce (illustrated)	303
HANNEY, P. W.	
The mosquitos of Zaria Province, Northern Nigeria (illustrated)	145
HARRIS, E.	
Distortion of guineacorn (<i>Sorghum vulgare</i>) caused by a mealybug, <i>Heterococcus nigeriensis</i> Williams, in Northern Nigeria (illustrated)	677
HOCKING, B.	
An insect-proof doorway (illustrated)	135

CONTENTS

PAGE

INGRAM, W. R.	
The control of yellow tea mite, <i>Hemitarsonemus latus</i> (Banks), with DDT on cotton in Uganda (illustrated)	577
JEPSON, W. F. & MATHIAS, P.	
The control of frit fly, <i>Oscinella frit</i> (L.), in sweet corn (<i>Zea mays</i>) by Thimet (O,O-diethyl S-ethylthiomethyl phosphorodithioate) (illustrated)	427
KERRICH, G. J.	
The forms of <i>Syntomosphyrum</i> (Hym., Eulophidae) parasitic on tsetse flies	21
KETTLE, D. S.	
The flight of <i>Culicoides impunctatus</i> Goetghebuer (Diptera, Ceratopogonidae) over moorland and its bearing on midge control (illustrated)	461
KIRBY, W. W. & BLASDALE, P.	
The eradication of <i>Glossina morsitans submorsitans</i> Newst. and <i>Glossina tachinoides</i> Westw. in part of a river flood plain in Northern Nigeria by chemical means. Part II (illustrated) ...	253
LAURENCE, B. R.	
The biology of two species of mosquito, <i>Mansonia africana</i> (Theobald) and <i>Mansonia uniformis</i> (Theobald), belonging to the subgenus <i>Mansonioides</i> (Diptera, Culicidae) (illustrated) ...	491
LEGGATE, B. M. & PILSON, R. D.	
The diurnal feeding activity of <i>Glossina pallidipes</i> Aust. in relation to trypanosome challenge (illustrated)	697
LEWIS, D. J.	
Observations on the <i>Simulium neavei</i> complex at Amani in Tanganyika (illustrated)	95
LONG, D. B.	
Larval movement and infestation in the wheat bulb fly, <i>Leptohylemyia coarctata</i> (Fall.) (illustrated)	405
MAELZER, D. A.	
The behaviour of the adult of <i>Aphodius tasmaniae</i> Hope (Col., Scarabaeidae) in South Australia (illustrated)	643
MILNE, A.	
Biology and ecology of the garden chafer, <i>Phyllopertha horticola</i> (L.). VII.—The flight season: male and female behaviour, and concluding discussion (illustrated)	353
MORRIS, K. R. S.	
Trapping as a means of studying the game tsetse, <i>Glossina pallidipes</i> Aust. (illustrated)	533
+ MUIR, D. A.	
A culture method for myrmecophilous root aphids (illustrated) ...	7
NORRIS, M. J.	
Group effects on feeding in adult males of the desert locust, <i>Schistocerca gregaria</i> (Forsk.), in relation to sexual maturation (illustrated)	731
+ ODHIAMBO, T. R.	
The identity of <i>Pseudodoniella laensis</i> Miller (Hemiptera, Miridae), associated with cacao in New Guinea and Papua (illustrated) ...	519

RIVNAY, E.	
The life-history of the melon weevil, <i>Baris granulipennis</i> (Tourn.) in Israel (<i>illustrated</i>)	115
SAUNDERS, D. S.	
The "white-clubbed" form of <i>Syntomosphyrum</i> (Hym., Eulophidae) parasitic on tsetse flies	17
+ SAUNDERS, D. S.	
On the stages in the development of <i>Syntomosphyrum albiclavus</i> Kerrich (Hym., Eulophidae), a parasite of tsetse flies (<i>illustrated</i>)	25
SAWICKI, R. M.	
A technique for the topical application of poisons to non-anaesthetised house-flies for knockdown assessments (<i>illustrated</i>) ...	715
SIMMONDS, F. J.	
Biological control of the coconut scale, <i>Aspidiotus destructor</i> Sign., in Principe, Portuguese West Africa (<i>illustrated</i>)	223
TAPLEY, R. G.	
The white coffee borer, <i>Anthores leuconotus</i> Pasc., and its control (<i>illustrated</i>)	279
VANDERPLANK, F. L.	
The availability of the coconut bug, <i>Pseudotheraptus wayi</i> Brown (Coreidae)	57
WALKER, P. T.	
Insecticide studies on the maize stalk borer, <i>Busseola fusca</i> (Fuller), in East Africa (<i>illustrated</i>)	321
WARD, J., GILLHAM, E. M. & POTTER, C.	
A thermal preference method of bioassay of the toxicity of insecticidal films to house-flies (<i>illustrated</i>)	379
WHEATLEY, P. E.	
Rearing <i>Pseudotheraptus wayi</i> Brown (Coreidae), a pest of coconuts in East Africa, and evaluation of its susceptibility to various insecticides	723
WHITEHEAD, G. B. & BAKER, J. A. F.	
Acaricide resistance in the red tick, <i>Rhipicephalus evertsi</i> Neumann (<i>illustrated</i>)	755
+ WILLIAMS, D. J.	
A new species of <i>Dysmicoccus</i> Ferris (Pseudococcidae, Homoptera) on banana (<i>illustrated</i>)	239
1961 + WILLIAMS, D. J.	
Notes on the genus <i>Heterococcus</i> Ferris (Coccoidea, Homoptera) with a description of a new species injurious to guineacorn (<i>Sorghum vulgare</i>) in Nigeria (<i>illustrated</i>)	671
WILLIAMS, J. B.	
The control of black sage (<i>Cordia macrostachya</i>) in Mauritius: the introduction, biology and bionomics of a species of <i>Eurytoma</i> (Hymenoptera, Chalcidoidea) (<i>illustrated</i>)	123
YEO, D. & SIMPSON, H. R.	
The effect of repeated insecticidal applications on a natural tsetse population	631
YULE, W. N.	
Dieldrin lattices applied by aircraft for controlling hoppers of the red locust, <i>Nomadacris septemfasciata</i> (Serville) (<i>illustrated</i>) ...	441

CONTENTS

DATES OF PUBLICATION IN PARTS

Part I	pp. 1-222	...	21 April 1960
Part II	pp. 223-414	...	29 July 1960
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ERRATA

- Page 23, line 6, for "*pallidipes*" read "*palpalis*"
- Page 74, 16 lines from end, omit "the"
- Page 75, line 5, for "accessary" read "accessory"
- Page 77, line 23 and page 78, line 16, for "*A. marshalli* var. *gibbinsi*" read "*A. marshallii* var. *gibbinsi*"
- Page 110, line 1, for "*Simulium neavi*" read "*Simulium neavei*"
- Page 110, 4 lines from end, for "indentifying" read "identifying"
- Page 160, fig 8, 2nd col., for "*M. africanus*" read "*M. africana*"
- Page 387, line 11, for "0.65" read "0.69"
- Page 441, line 1, for "*Nomadacris septemfasciata*" read "*Nomadacris septemfasciata*"
- Page 495, line 46, after "starved" insert "of a blood-meal"
- Page 684, line 4, for "other" read "otherwise"
- Page 723, line 1 (title), insert comma after "(Coreidae)"
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A SPEAR FOR SAMPLING BULK GRAIN BY SUCTION.

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E.M.N.

(PLATE I.)

In the study of the ecology of insects in bulks of stored grain, a large number of big, deep samples is usually required for the estimation of the insect population and the moisture content of the grain. Early types of grain-sampling spear are pushed into the bulk from the top and opened to allow a sample of grain to fall into them under its own weight (*e.g.*, Pl. I, fig. 1). This method of sampling has a number of serious disadvantages. The spears usually hold only small samples and many models remain open while being pulled out of the bulk. All are difficult to use if the direction of insertion is at an angle to the vertical and they cannot be used horizontally or upwards. Samples cannot be obtained from directly against the walls or from very near the floor of a store. Since the spears are comparatively wide in cross-section, considerable force is needed to push them into the grain. One or more of these limitations frequently prevents the sampling of the more interesting or important regions of a bulk.

Later types of spear are cumbersome, long and narrow, and they have the same method of filling (*e.g.*, Lucas & Glover, 1946). They can be closed before they are pulled out of the bulk, and they hold bigger samples, but they are suitable for use only in the most accessible stores, such as some silos.

By sucking a sample out of a bulk through a pipe with the apparatus described in this paper, most of the above disadvantages can be eliminated.

Apparatus.

The apparatus is illustrated in Plate I, figs. 2 & 3. It consists of a spear-device on the end of a sampling pipe, a sample container and an ordinary large, domestic vacuum cleaner. These parts are all connected together, allowing an air stream generated by the vacuum cleaner to draw a sample of grain through the pipe into the container.

It is desirable to keep the apparatus as narrow as possible while avoiding jamming of the grain and undue reduction of the speed of the air stream. All the measurements given below are the smallest that should be used to sample wheat or malted barley with the given rate of air flow. The apparatus has been tested only in these two cereals, but it is believed to be suitable for all grains no longer and no wider than barley. It could probably be adapted to longer or wider grains by increasing the internal diameter of the pipe and of all other parts through which the grain flows.

The spear comprises an inner tube and an outer sleeve as shown in fig. 1. The inner tube is 1.6 cm. in diameter. One end is firmly attached to the sampling

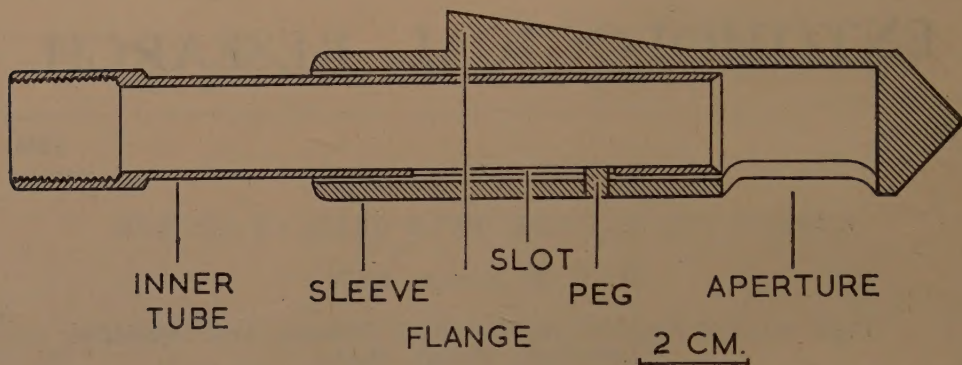


Fig. 1.—A section through the spear of the suction sampling apparatus.

pipe by a screw thread, the other is open. The outer sleeve slides freely over the inner tube, but its travel is limited by a peg in the sleeve projecting into a slot in the inner tube. The outer sleeve is bluntly tapered at the free end, with a rectangular aperture, 2.8 cm. high by 2.0 cm. wide, cut in the side immediately above the taper (fig. 1). The travel allowed the sleeve is just sufficient either to close or fully uncover the aperture. Above the aperture, another taper leads to a flange, 0.7 cm. wide, which is cut away above the aperture.

In use, the spear is kept closed, during insertion, by the resistance of the grain. When the desired sampling point has been reached, the aperture in the sleeve is opened by jerking back the sampling pipe a little. This slides back the inner tube of the spear and, as the sleeve is prevented from moving by the grain gripping the flange, the aperture is opened. The cut-away portion of the flange (see Pl. I, fig. 2) allows insertion very near a wall.

The pipe (Pl. I, fig. 2) is $\frac{1}{2}$ inch gas pipe, which is stout-walled with an internal diameter not less than that of the spear. Short sections are screwed together as the pipe is pushed into the grain. Insertion of the pipe can be facilitated by screwing a cross-piece temporarily on to the top section.

As soon as the spear has been inserted to the required distance, the top of the pipe is connected to the glass sample container. This is a '3-lb. kilner' jar with the glass lid replaced by a metal one, into which are fixed two lengths of $\frac{3}{4}$ inch (external diameter) flexible conduit. One conduit connects on to the pipe by means of a union coupling, the other bears a tapered adaptor, which fits into the vacuum cleaner. A filter of metal gauze (23 meshes to the centimetre) is fixed on the lid of the sample container over the outlet conduit (Pl. I, fig. 3). This prevents all material, except fine dust and possibly some mites and the smallest stages of some insects, from passing into the vacuum cleaner.

Without the apparatus attached, the vacuum cleaner generates a suction of

129 cm. water gauge (at sea-level, closed) and it has a through-put of air of 23.6 l./sec. (at sea-level, open).

Operation and performance.

For insertion of the spear into a bulk of grain a number of jerks are much more effective than a continuous thrust. In this manner the spear has been pushed by one operator to a depth of more than 9 m. into malted barley of 2 per cent. moisture content. When a sufficient sample of grain has been sucked into the sample container with the pipe inserted from above, the vacuum cleaner is switched off, allowing the grain which was ascending the pipe to fall. If the vacuum cleaner is switched on again, the suction is not powerful enough to lift the stationary column of grain accumulated at the bottom of the pipe, consequently the pipe must be withdrawn and emptied before the next sample can be taken. Although this is laborious, it has the advantage of allowing both the pipe and the spear to be reattached to the vacuum cleaner and cleaned thoroughly with a strong air stream. During cleaning, the outer sleeve of the spear should be jerked up and down several times to release the dust, which tends to collect between the outer sleeve and the inner tube while the sample is being sucked from the bulk, and which, if allowed to accumulate, may cause the spear to jam.

A series of samples taken successively at intervals of 1 to 2 m. along a straight line reduces the compactness of the grain and allows the spear to be inserted easily. Since grain of a higher moisture content than malt offers greater resistance, particularly if caking has taken place, such a series of samples may be essential to facilitate penetration deep into the bulk, as well as giving useful information. The apparatus has been successful with the pipe inserted into bulk malt either downwards, horizontally or slightly upwards. It should also be possible to use it vertically upwards, possibly without cleaning the spear between successive samples.

The vacuum cleaner in use generated sufficient suction to lift malt 8 to 9 m.

The size of the sample is limited only by the size of the container, which can be filled completely if necessary. To simplify the apparatus, the 'dirt bag' of some vacuum cleaners can be used as a sample-container by connecting a flexible tube directly from the pipe to the cleaner.

During trials with wheat in a glass tank, it was observed that grain immediately in front of the aperture in the spear ascended first, then grain tended to fall downwards to fill the vacated space, so that finally the sample was extracted from a region between the bottom of the aperture and about 10 cm. above it. Consequently the aperture should be positioned in the bulk about 5 cm. below the required sampling point. It is possible to sample a layer of grain extending from 1 to 10 cm. above the bottom of the bulk. A sample can be obtained from directly against a wall by inserting the spear with the aperture close to and facing the wall. A traverse can be made by withdrawing the pipe steadily during the act of sampling and by using a deeper sample container. The first grain sucked up the pipe falls to the bottom of the container and the last grain lies at the top, so that the depth of the grain itself in the container should be representative of position along the traverse, but the *débris* will be mixed, since it tends to collect around the filter.

It might be expected that fine, light *débris* would be sucked up the pipe more rapidly, and withdrawn from a larger space, than the bigger and denser cereal grains. Therefore, samples were taken with the suction spear and with an early, conventional sampling spear from points in a bulk of malted barley as close together as could be achieved. The conventional spear was a large cargo sampler (Pl. I, fig. 1), holding about 115 g. of malt. The 'suction' samples weighed about 550 g. The suction samples contained a higher proportion of *débris* than

the conventional ones from four points and a lower proportion from three (Table I). The difference could not be related to the depth from which the sample was collected or to the amount of débris obtained. The mean value of this proportion was a little greater for the suction samples than for the conventional ones, but the difference was not significant ($P = 0.2$, using a 't' test for paired values,

TABLE I.

The percentage by weight of débris passing a sieve of 4 meshes to the cm. in samples taken with a conventional spear and with a suction spear.

Position	Depth (m.)	Conventional sample (C)	Suction sample (S)	Difference (S-C)
A ..	0.3	0.30	0.33	+ 0.08
A ..	0.6	0.21	0.33	+ 0.12
A ..	0.9	0.39	0.37	- 0.02
A ..	1.2	0.54	0.57	+ 0.03
A ..	1.5	0.46	0.41	- 0.05
B ..	0.6	0.73	0.95	+ 0.22
C ..	0.6	0.70	0.67	- 0.03
Mean	—	0.48	0.53	+ 0.05

following Snedecor, 1956). It can be concluded that the suction spear is, at worst, only very slightly selective, with grain containing less than 1 per cent. of débris.

Since material is sucked into the container with considerable force, there is a risk that insects in the sample may be damaged. It was observed, however, that larvae older than the first instar and adults of the khapra beetle, *Trogoderma granarium* Everts, were not injured, even though the larvae are fairly soft-bodied. Pre-adult stages of species with softer bodies, also first-instar larvae and eggs of *Trogoderma*, would probably be damaged. Insects in samples taken from deep points should not be harmed, because these samples are sucked into the container fairly slowly. If damage is feared, the velocity of the air stream can be decreased by fixing an adjustable baffle over the outlet hole of the vacuum cleaner.

Summary.

A light-weight spear has been developed to take samples of unlimited size from bulks of cereal grains. The spear is screwed on to lengths of narrow metal pipe, which are used to insert it into a bulk of grain. The sample is sucked out of the bulk through the pipe by the air stream of a domestic vacuum cleaner. This method largely overcomes the disadvantages inherent in other types of spear. The spear can be inserted into a bulk in any direction, even upwards. When sampling downwards, samples can be obtained from as deep as 9 m. Samples can be taken from directly against the walls of a store and as close as 1 cm. to the floor.

Acknowledgements.

Mr. M. A. Cordaroy made the apparatus and gave valuable assistance in design. This work formed part of the research programme of the Pest Infestation Laboratory and this account is published with the permission of the Department of Scientific and Industrial Research.

References.

LUCAS, C. E. & GLOVER, R. S. (1946). On making measurements in silo-stored grain.—*Ann. appl. Biol.* **33** pp. 293–302.

SNEDECOR, G. W. (1956). Statistical methods applied to experiments in agriculture and biology.—5th ed., 534 pp. Ames, Iowa, Iowa St. Coll. Pr.



FIG. 1. A conventional sampling spear ($\times 0.18$).

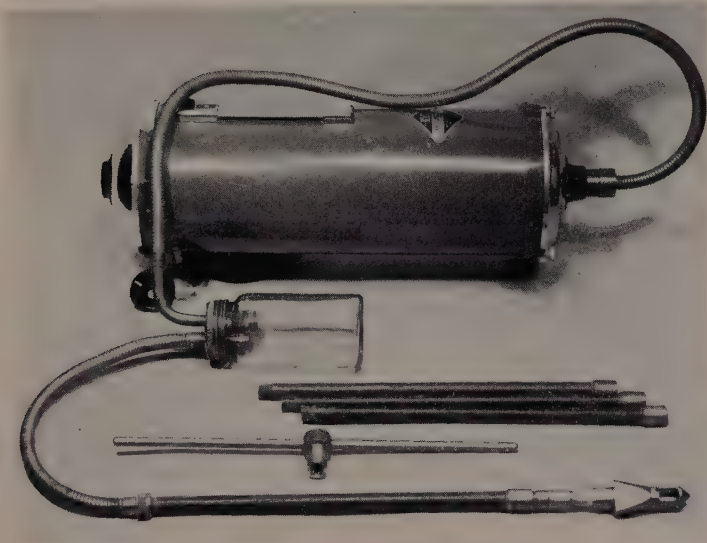


FIG. 2. Suction sampling apparatus ($\times 0.063$).

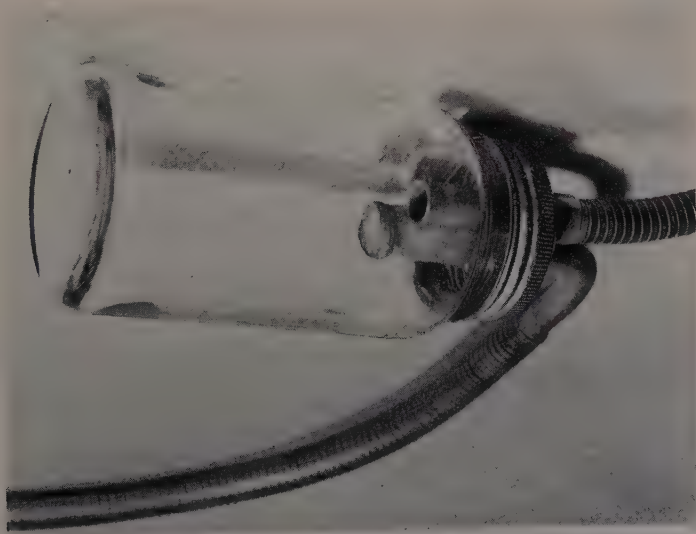


FIG. 3. Details of the air filter in the lid of the container ($\times 0.28$).

A CULTURE METHOD FOR MYRMECOPHILOUS ROOT APHIDS.

By D. A. MUIR

E.M.N.

Zoology Department, University of Glasgow.

In the course of recent investigations of the association of ant colonies with subterranean aphids, it became necessary to develop a suitable method of culturing the latter in order to facilitate experimental work.

The system evolved is as follows: The host-plant may be grown in a liquid medium or soil, as desired, and its container varied accordingly. A piece of root or rhizome is exposed and bent into a loop which is then inserted into one end of a piece of glass tubing of suitable diameter and length, care being taken that the root or rhizome is not warped by undue pressure. The end of the tube through which the plant material enters is then plugged with cotton-wool. The aphids are introduced and the other end plugged in turn (fig. 1).

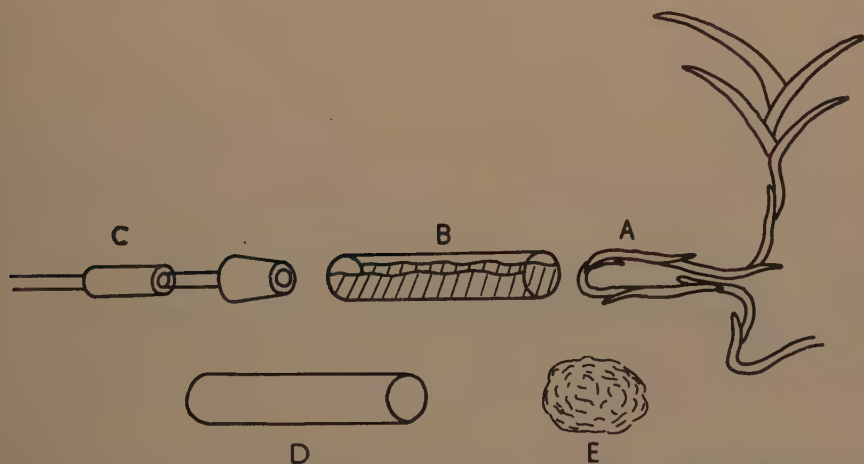


Fig. 1.—Components of aphid cell. A, plant loop; B, glass cell with plaster lining; C, connecting glass tubing with rubber joint and stopper; D, opaque plastic sleeve; E, cotton-wool plug.

Humidity is maintained by evaporation from the plant loop, and may be regulated by adjusting the compactness of the cotton-wool plugs. In order to minimise the risk of any wandering aphids being trapped by condensation droplets on the tube wall, it is advisable to line this partially with a thin film of plaster of paris, leaving a strip bare for the purposes of observation. The whole culture cell is covered finally with a black plastic sleeve.

Ant colonies are maintained in normal two-chambered plaster nests as described by Brian (1951). When it is desired to make the aphid culture available to a laboratory ant colony, rubber-jointed glass tubing is used as a connection, one end being plugged into the aphid cell by a suitably sized and bored stopper, after removal of the cotton-wool plug, the other end being plugged into a hole

drilled through the side of the plaster nest. Ant access may be controlled conveniently by a plastic strip running in a slot cut in the plaster across the exit hole (fig. 2).

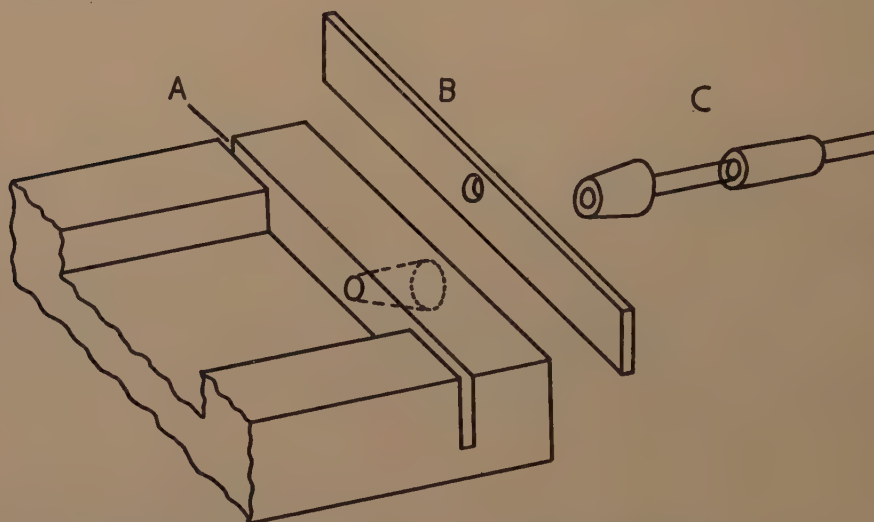


Fig. 2.—End of plaster nest for ants, showing exit hole and modifications. A, slot in plaster for plastic strip; B, plastic strip; C, connection with aphid cell.

The cultural system described thus possesses the following desirable features: damage to the host-plant is at a minimum; the aphid cell may be connected to successive ant colonies with no disturbance of aphids or ants; a cell may be quickly and easily transferred to a fresh site with no disturbance of any attached ant colony.

Similar culture cells may be devised for aphids feeding on the aerial parts of the plant by adaptation of the bivalve cage described by Hill (1955).

References.

- Net: RAE B. BRIAN, M. V. (1951). Ant culture for laboratory experiment.—*Ent. mon. Mag.* 87 pp. 134–136.
- Net: RAE HILL, A. R. (1955). A bivalve cage for small arthropods.—*Proc. R. ent. Soc. Lond. (A)* 30 pp. 167–168.

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OBSERVATIONS ON *SIMULIUM NEAVEI* ROUBAUD, WITH SPECIAL
REFERENCE TO A FOCUS OF ONCHOCERCIASIS IN THE
BELGIAN CONGO.

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26

(PLATE II.)

The clinical investigation of onchocerciasis in a district in the Oriental Province of the Belgian Congo (Browne, 1960), is supplemented by this study of *Simulium neavei* Roub., the vector concerned.

The district in question is situated in the tropical rain-forest, just to the north of the Equator, and mainly between 23° and 25°E.; it has an altitude of between 1,350 and 1,650 ft. (410–480 metres). The annual rainfall varies from 50 to 85 in. (1270–2160 mm.), and the average daily maximum and minimum temperatures are 86 and 70°F. (30 and 20°C.), respectively. The average relative humidity, 98 per cent. at dawn, falls to 70 per cent. at midday. There is but little seasonal variation in rainfall, temperature and humidity, though the months of December–January and July–August tend to be less wet, and the heaviest rains occur in March and November. Apart from considerable areas of wooded marsh, the surface of the land is irregularly undulating, with scattered low hills, separated by ravined watercourses, the whole covered with primary or secondary forest.

Clinical or pathological evidence of onchocerciasis was found in the inhabitants of the great majority of river and forest villages throughout the district, though Simuliids were confined to well-recognized areas. There has recently been much travel from village to village, by forest roads and by canoe. In villages distant from known Simuliid areas, the incidence of onchocerciasis was under 1 per cent. In the central villages of the two principal foci of the disease, all the adult inhabitants were infected.

The Bokuma focus abuts on to the southern bank of the River Congo; very numerous streams (17 in a stretch of 12 miles (19 km.)) slow considerably and broaden slightly before they enter, separately, the main river, in which the seasonal variation in level may reach 15–18 ft. (4.6–5.5 metres). Within this focus, extensive clearings have been made of recent years for coffee and rubber plantations.

The Bembelota focus is situated some 20 miles south of the main river, to the west of the River Lomami, and to the north of an uninhabited forest corridor. Small, scattered clearings for temporary gardens, and larger clearings for plantations, are to be found in the forest. The unmapped network of streams flows into several main channels which eventually enter a tributary of the main river; some smaller streams are lost in the slow-moving waters of marshy expanses between villages to the north.

There is generally little air movement in the rain-forest, apart from the violent disturbances accompanying the frequent tropical storms.

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The vector.

All the female Simuliids found biting human bait and despatched to the British Museum (Natural History) (where they were kindly identified by Dr. Paul Freeman), were found to be *S. neavei*.

No Simuliids were caught in the wattle-and-daub huts of the villagers; or in the houses of the workpeople (made of sun-dried brick, with corrugated cement plaque roofs), or on the verandahs of the latter. About 10 per cent. of the flies biting human bait were captured near houses in the shade of bushes and elephant grass. Only 2 per cent. were found near watercourses. The rest were taken biting human bait in the forest clearings up to a mile distant from streams, especially near coffee bushes.

Workmen on several independent occasions volunteered the information—and demonstrated its truth—that vigorous disturbance of loose decaying vegetation and humus under felled and rotting trees in young plantations would be followed by the alighting of Simuliids on the calves and ankles. The flies were aggressive and voracious throughout the hours of daylight, but especially from 7.30 a.m. to 10 a.m. and from 4 p.m. to 5.30 p.m. There seemed to be an increase in the fly population in June to August, with perhaps an increase in aggressiveness. For some years, there had probably been a steady increase in the total fly population, corresponding to the arrival of workmen and their families.

As the plantation rubber trees grew in height, so biting by *Simulium* in their vicinity diminished; but near the pruned coffee bushes (with their multiple low branches covered with thick leaves), where workmen remained hoeing, pruning and making compost trenches for many minutes, no decrease was noted.

As a rule, Simuliids were not found biting far from the shade, and rarely crossed a sunlit zone of denuded earth. They bit as freely on bright days as on dull, but avoided the brightest sunlight and the midday hours.

Dissection of females of *S. neavei*.

A small series of 239 Simuliids, caught biting human bait—the majority in forest clearings—was dissected. Only 12 were found to harbour developmental forms of *Onchocerca volvulus* or somewhat similar nematodes. Reported percentages of infected Simuliids vary considerably, from 2.6 (Blacklock, 1926) and 5.0 (Strong & others, 1934), to 3–15 (Wanson & Hennard, 1945), and 7.3–18 (Van den Berghe, 1941) and even 88 (McMahon, 1940).

Mature infective forms were found in the thoracic muscles of one specimen of *S. neavei* (and none in the head); 18 early sausage forms were found, and 44 late sausage forms. These figures are admittedly too small to serve as a basis for valid conclusions, but may be typical.

Anatomical sites bitten by *S. neavei*.

No Simuliids were found biting the face or scalp, even when the human bait was lying down, and none were found on animals or birds used as bait. Of all the bites recorded 85 per cent. were on the knees or below, particularly in the sulci on either side of the Tendo Achilles; 10 per cent. below the level of the umbilicus and above the knees (including the hands and forearms when dependent), and the remaining 5 per cent. on the upper trunk, arms and shoulders. The localization of onchocercemata in this district corresponds to the sites of inoculation of the larval filariae (Browne, 1960).

Breeding places in the Bokuma focus.

Egg clusters were found adherent to underwater objects (limonite stones principally, occasionally decaying branches) in delimited stretches of fast-flowing streams. The clusters numbered 200–300 closely bound eggs, ranging in colour

from dark cream to dark brown: magnified, they were seen to be triangular with rounded angles and appeared identical with Simuliid eggs described and figured by Brumpt (1949), and by Crisp (1956). The following conditions were present in all places where these eggs were found: clear water, six to nine inches deep, flowing over beds composed of rock, or pebbles or clean sand; and moderately shaded, tree-lined banks (Pl. II, fig. 1). In a single stretch of two yards of a stream ten feet wide, forty clusters of eggs were found. Oviposition was not observed, neither was hatching of larvae from eggs.

Despite prolonged search in these sites and down-stream, no Simuliid larvae or pupae were found on any underwater object examined, inanimate or living (crabs, snails, fish, mayfly nymphs, etc.). In particular, hundreds of crabs taken from the streams and the main river (which here flows at about 3 km. per hour (2.75 ft. per second)) were inspected, with negative results.

When, however, the higher and less accessible reaches were systematically investigated at selected points, larvae and pupae were at length discovered on crabs taken from localized stretches of several streams, and clusters of eggs similar to those described above were found on limonite stones. No larvae or pupae were found on objects other than crabs. The very numerous Simuliids would seem to have passed their intermediate stages on a relatively small number of crabs. No crabs were seen on dry land, and no crabs with larvae were found in marshy water.

In the Bokuma focus, 11 streams were found to be infested: many crabs harboured larvae or pupae, or both, while others taken from neighbouring stretches were free of both. In the adjacent sites, the physical features of the banks and

TABLE I.

Distribution of larvae of *S. neavei* on crabs.

Site					Totals
Carapace :					178
Superior surface	16		
Inferior surface	<u>149</u>	165	
Near mouth		2	
Attached to eye stalks		<u>11</u>	
Chelipeds :					111
First segment		50	
Second "		51	
Third "		<u>10</u>	
Walking legs :					240
Segments	1st	2nd	3rd		
1st pair	49	4	1		
2nd "	81	6	1		
3rd "	58	7	2		
4th "	27	4	0		
	<u>215</u>	<u>21</u>	<u>4</u>		
Grand Total					529

N.B.—Numbering of segments is from the basal outwards to the distal.

beds and local climate were very similar; the crabs were found in the water under the over-hanging, moss-grown banks and exposed roots, and lurking beneath decaying submerged branches, especially when festooned with entrapped leaves and living weeds. The forest was similarly dense in both situations, usually meeting overhead and admitting only a diffuse light even at midday. The water appeared similar in every respect: clarity, colour, suspended solids and depth; the temperature was 24–27°C.

The only difference discovered was that the crabs with larvae or pupae attached were found in those stretches of water where the current flowed at $3\frac{1}{2}$ to 7 km. per hour (3.2 to 6.4 ft. per sec.).

In one series of observations, 101 crabs were found with larvae or pupae: 72 had larvae, and 63 had pupae. The larvae were distributed on the crabs as shown in Table I.

In view of the discovery of another member of the *neavei* complex (*S. woodi* De Meillon) in the exhalant passages of crabs (McMahon, 1957a), these passages were examined, with negative results.

TABLE II.

Occurrence of larvae or pupae of *S. neavei* on crabs of differing transverse carapace diameter.

Transverse carapace diameter (cm.)	Larvae or pupae		<i>Simulium</i> present (%)
	Absent	Present	
2.0	115	1	2.4
.2	91	1	
.4	88	0	
.6	68	4	
.8	58	4	
3.0	41	1	8.7
.2	59	3	
.4	52	6	
.6	56	3	
.8	46	9	
4.0	68	5	7.2
.2	51	0	
.4	62	2	
.6	42	6	
.8	56	7	
5.0	71	11	16.8
.2	46	9	
.4	80	13	
.6	69	7	
.8	43	12	
6.0	51	13	24.2
.2	33	6	
.4	26	4	
.6	10	4	
.8	4	3	
7.0	7	4	54.5
.2	3	1	
10.0	1	1	
	11	6	
	1397	140	10.0%

The larvae blended well with the colouring of the crabs, and care was needed to detect them, especially when they lay curled near the origin of the appendages.

No eggs were found on crabs; but empty Simuliid cocoons were noted in large numbers.

In an attempt to ascertain the optimum sizes of crabs for the association between them and the larval and pupal stages of *S. neavei*, the largest transverse measurement of the carapace was taken of all crabs in one series, with the results shown in Table II.

Many hundreds of smaller crabs were examined, but no larvae or pupae were found on crabs of less than 2 cm. transverse carapace diameter. Pupae were generally less numerous than larvae: the average number of larvae per crab was 7.3; on one crab there were no fewer than 55. Of the ten infested crabs of less than 3 cm. carapace diameter, nine came from three adjacent streams. No very small larvae were found. On individual crabs, the larvae were usually of the same length; rarely, a single crab harboured larvae of differing lengths. Pupae were found in similar situations to the larvae.

(An interesting, but unconnected observation was made in the course of routine examination of the crabs: on the carapaces, chelipeds and walking legs of many of the crabs, there were numerous empty cocoons presumed to be those of oligochaet worms, very different from Simuliid cocoons, being smaller, flattened, fusiform structures. Up to two or three hundred were counted on a single crab. After many fruitless examinations, two cocoons were found containing living oligochaetes, kindly identified by Mr. N. Tebble, of the British Museum).

Identification of the crabs.

Many crabs from the different streams in both the Bokuma and the Bembelota foci were despatched to the British Museum (Natural History), where they were identified by Dr. I. Gordon.

The most numerous is to be referred to as *Potamon* (*Potamonautes*) sp. while the definitive revision of the Congo POTAMONIDAE is awaited; others were:

- Potamon* (*Potamon*) *ballayi* (A.M.-Edw.);
- Potamon* (*Potamonautes*) *lirrangensis* Rathbun;
- Potamon* (*Potamonautes*) *stanleyensis* Rathbun;
- Potamon* (*Potamonautes*) *langi* Rathbun.

These five species were all collected from streams in the Bokuma focus within a radius of a few miles; some species seemed to be confined to single streams.

Treatment of streams.

In the absence of detailed maps of the district containing the Bokuma focus, charts were prepared showing the disposition of the mouths and approximate courses of the streams; paths were subsequently cut through the forest to the streams above the observed breeding places of *S. neavei*.

The speed of the current at each of the breeding places was ascertained by pouring rapidly 100 ml. of 1 per cent. aqueous methylene blue into the stream from points marked at 1-metre intervals on a string suspended from bank to bank, and timing the tinted water as it passed under another string suspended at a measured distance downstream.

The depth of the water was measured at each 1-metre marking on the first stretched string (Pl. II, fig. 2), and note made of the condition of the bed.

With the assistance of tables from McMahon's valuable paper (1957b), the discharge for each stream was calculated from the hydraulic mean depth and the constants for water flow in earth channels.

Empty 8-gallon petrol drums were pierced with holes of such calculated diameter that the contents of the drum would on discharge produce a concentration of larvicidal solution of one part per 500,000 for 30 minutes at the breeding site. The solution employed was Neocide M 25 (Geigy) (which consists of 25% DDT; 70% of a solvent derived from aromatic paraffin; 5% of inert substance), made into an emulsion by the slow addition of water, with constant stirring.

Each infested stream in the western half of the Bokuma focus was treated at 10-day intervals for ten applications.

A census of crabs from each treated stream showed that the solution was lethal to larvae and pupae of *Simulium*, but not to the crabs. Small dead fish were found floating past the breeding places, the concentration of larvicide in the upper reaches having been lethal for them.

Within the next two or three months, the adults of *Simulium neavei* were greatly reduced in numbers and almost disappeared, though the complete eradication recorded by Garnham & McMahon (1947; 1954) was not attained. Four months later, it was somewhat disquieting, though not altogether unexpected, to discover larvae and pupae on isolated crabs taken from three streams out of the eleven treated. Surviving Simuliids, or Simuliids entering the area from distant breeding places (known and suspected) accounted for the reinfestation; in view of the high mortality of developmental forms of *S. neavei*, it was still hoped that the infestation could be reduced below the critical level for survival of the insect within the focus in this pilot experiment. This hope has been partially justified, and further periodical larvicidal treatment of the streams formerly heavily infested are being made. The African workpeople and their families, as well as the Europeans interested economically in the development of the plantations, agree that the decided reduction in the Simuliid population is most welcome.

The Bembelota focus.

The problem here seems insoluble, by reason of the terrain. The three villages where the incidence of onchocerciasis is highest are situated near the uninhabited forest corridor, over 20 miles from the main road. The numerous streams in the neighbourhood are situated in dense primary forest.

All the Simuliids taken biting human bait are *S. neavei*.

Over 2,000 crabs from the accessible stretches of numerous watercourses have been examined, but only three larvae and two pupae have been found on carapaces, pincers and walking legs; none has been found in the exhalant passages or elsewhere, and none has been found on any other underwater objects examined. The breeding places remain to be found in stretches of streams in unexplored primary rain-forest to the south.

Summary.

Parts of a district situated in the tropical rain-forest of the Belgian Congo in which onchocerciasis was generally endemic, were investigated to identify the vector and to ascertain its phoretic host, breeding places, habits, etc.

The vector found biting human bait (usually less than 1 metre from the ground) was *Simulium neavei* Roub. Dissection of adult females revealed developmental forms of *Onchocerca volvulus*.

Larvae and pupae were found on crabs of the genus *Potamon* in fast-flowing stretches of the numerous small streams flowing into the River Congo.

The infested streams in the main focus of onchocerciasis were treated by DDT emulsion at a concentration of one part per 500,000 for 30 minutes, every ten days for ten applications.

The good results observed initially were partly offset by the reappearance six

months later of small numbers of Simuliids apparently developing from eggs laid by females entering the disinfested area from without.

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References.

- BLACKLOCK, D. B. (1926). The development of *Onchocerca volvulus* in *Simulium damnosum*.—*Ann. trop. Med. Parasit.* **20** pp. 1-48.
- BROWNE, S. G. (1960). Incidence and clinical manifestations of onchocerciasis in a focus in the Oriental Province of the Belgian Congo.—*Ann. trop. Med. Parasit.* **53** pp. 421-429.
- BRUMPT, E. (1949). Précis de parasitologie.—6th edn., 1042 pp. Paris, Masson.
- CRISP, G. (1956). *Simulium* and onchocerciasis in the Northern Territories of the Gold Coast.—171 pp. London, Brit. Emp. Soc. Blind & H. K. Lewis.
- GARNHAM, P. C. C. & McMAHON, J. P. (1947). The eradication of *Simulium neavei* Roubaud, from an onchocerciasis area in Kenya Colony.—*Bull. ent. Res.* **37** pp. 619-628.
- GARNHAM, P. C. C. & McMAHON, J. P. (1954). Final results of an experiment on the control of onchocerciasis by eradication of the vector.—*Bull. ent. Res.* **45** pp. 175-176.
- McMAHON, J. P. (1940). *Onchocerca volvulus* and its vector in the South Kavirondo district of Kenya.—*Trans. R. Soc. trop. Med. Hyg.* **34** pp. 65-83.
- McMAHON, J. P. (1957a). Notes on the *Simulium neavei* group of Simuliidae with particular reference to *S. nyasalandicum* and *S. woodi*.—*Bull. ent. Res.* **48** pp. 607-617.
- McMAHON, J. P. (1957b). DDT-treatment of rivers for eradication of Simuliidae.—*Bull. World Hlth Org.* **16** pp. 541-551.
- STRONG, R. P., SANDGROUND, J. H., BEQUAERT, J. C. & MUÑOZ OCHOA, M. (1934). Onchocerciasis with special reference to the Central American form of the disease.—*Contrib. Dep. trop. Med.* no. 6, 234 pp. Cambridge, Mass., Harvard Univ. Pr.
- VAN DEN BERGHE, L. (1941). Recherches sur l'onchocercose au Congo Belge. 1er mémoire.—*Ann. Soc. belge Méd. trop.* **21** pp. 63-76.
- WANSON, M. & HENRARD, C. (1945). Habitat et comportement larvaire du *Simulium damnosum* Theobald.—*Rec. Trav. Sci. méd. Congo belge* no. 4 pp. 113-121.



FIG. 1. Typical stretch of stream in which numerous clusters of unidentified eggs but no Simuliid larvae or pupae were found.



FIG. 2. Estimating rate of flow and discharge in a breeding place of *Simulium neavei* preparatory to application of larvicide.

THE 'WHITE-CLUBBED' FORM OF *SYNTOMOSPHYRUM* (HYM., EULOPHIDAE) PARASITIC ON TSETSE FLIES.

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Waterston (1915), in describing the type female of *Syntomosphyrum glossinae*, states: "In no region is the antenna really black, but the funicle and club are dusky." The same author (Waterston, 1916) later examined some female specimens of *Syntomosphyrum* that had emerged from a puparium of *Glossina morsitans* Westw. collected in Nyasaland by W. A. Lamborn. These parasites had white-clubbed antennae and have been called the 'Nyasaland form' of *S. glossinae*. The males of the two forms appeared identical.

A laboratory study of the biology of these forms was carried out in London with material obtained from tsetse pupae sent from Africa. Specimens examined at the British Museum (Natural History) and at the London School of Hygiene and Tropical Medicine were found to include individuals with dark-clubbed antennae and others with white-clubbed antennae. The literature was also examined but no other reference to the 'white-clubbed' form could be found. There is evidence, however, that this was the form of *Syntomosphyrum* studied by Lamborn (1916, 1925) as it was he who supplied the 'white-clubbed' specimens described by Waterston (1916).

This paper deals with the results of attempted cross-mating experiments between the 'white-clubbed' and 'dark-clubbed' forms and discusses the taxonomic status of the former.

Materials and methods.

Examples of the 'white-clubbed' form, used in the present investigation, emerged from puparia of *G. morsitans* collected at Singida, Tanganyika. Typical (dark-clubbed) examples of *S. glossinae* were obtained from *G. pallidipes* Aust. from Kiboko and Makueni, Kenya, and from *G. palpalis* (R.-D.) and *G. morsitans submorsitans* Newst. collected near Kaduna, Northern Nigeria.

Lamborn (1925) showed that *Syntomosphyrum* will readily breed in blowfly pupae. In the present investigation the parasites were reared in pupae of *Lucilia sericata* (Mg.), thus obviating the difficulties involved in maintaining a laboratory supply of *Glossina*. The three strains of parasites were kept in separate perspex cages at about 25°C. and supplied with honey and fresh blowfly pupae. After a few hours' exposure to the parasites, the pupae were removed and incubated at 25°C. until the emergence of the offspring. Some of the parasites were used to restock the cages, thus ensuring a continuous emergence of *Syntomosphyrum*.

Males of *Syntomosphyrum* normally copulate with females from the same host puparium almost immediately after escaping from it. Therefore, in the crossing experiments, the pupae were removed from the host before they emerged, and isolated in specimen tubes to prevent unwanted sib matings. Virgin females of the 'dark-clubbed' form (from both Kenya and Nigeria) were placed singly in tubes with a male from a brood containing 'white-clubbed' females. Similarly, crosses were manipulated between 'white-clubbed' females and males of the two

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'darked-clubbed' strains. Puparia of *Lucilia* were placed in each tube, replaced daily and incubated at 25°C. The numbers and sex of the progeny were noted at emergence.

Results.

Nash (1933) observed that eggs laid by virgin females of *S. glossinae* produced all-male progeny, but that the progeny of mated females included both sexes. It is probable that reproduction in *Syntomosphyrum* resembles that of *Bracon* (cited as *Habrobracon*) (Torvik-Greb, 1935) and the honey bee (Vandel, 1931), in which the males are usually haploid and produced from unfertilised eggs and the females are diploid and from fertilised eggs.

In 20 crosses between males of the 'white-clubbed' form and typical females from Kenya, from 0 to 101 male progeny (mean, 44.3), but no female progeny, were produced (Table I). Similarly, females from any mating between the typical form (whether from Kenya or Nigeria) and the 'white-clubbed' form produced

TABLE I.

The results of cross-matings between three strains of *Syntomosphyrum*.

Cross	Number of crosses	Length of life* of male (days)	Sex ratio ($\delta\delta$: $\varphi\varphi$) of offspring
1. 'White-clubbed' $\delta\delta$ Kenya $\varphi\varphi$	20	3-20 (7.9)	0 : 0-101 : 0 (44.3 : 0)
2. Kenya $\delta\delta$ 'White-clubbed' $\varphi\varphi$	10	4-5 (4.2)	90 : 0-195 : 0 (144.2 : 0)
3. 'White-clubbed' $\delta\delta$ Nigeria $\varphi\varphi$	10	4-5 (4.5)	0 : 0-199 : 0 (130.8 : 0)
4. Nigeria $\delta\delta$ 'White-clubbed' $\varphi\varphi$	10	5 (5.0)	0 : 0-130 : 0 (72.3 : 0)
5. Kenya $\delta\delta$ (a) Nigeria $\varphi\varphi$ (b)	7 10	3 (3.0) 3-7 (4.0)	46 : 0-186 : 0 (90.6 : 0) 2 : 27-58 : 59 (9.8 : 49.3)

* indicates the length of time in which copulation could occur.

Figures in brackets represent mean values.

The 'white-clubbed' form was obtained from Tanganyika. The populations obtained from Kenya and Nigeria consisted of the typical, 'dark-clubbed' form.

all-male broods. Female offspring resulted only from crosses between the Kenya and Nigerian strains, both of which were of the 'dark-clubbed' form. In every experiment, the males lived long enough to copulate with the females and copulation behaviour was observed between the different strains. It would seem, therefore, that fertilisation occurred only in crosses between the Kenya and Nigerian strains and not in those involving males or females of the 'white-clubbed' form.

Discussion.

S. glossinae is recorded as occurring in East and West Africa and as a parasite of *G. morsitans*, *G. palpalis*, *G. pallidipes* and *G. brevipalpis* Newst. The few records that give any indication of the colour of the tip of the antenna in the

female show that the typical form is a parasite of *G. palpalis* in Uganda (Waterston, 1915); it is so in Nigeria (material received during the present investigation). Other definite records of the typical form are from *G. morsitans* in Tanganyika (material in the London School of Hygiene and Tropical Medicine) and Nigeria, and from *G. pallidipes* in Kenya (the last two records having been obtained during the present investigation). The 'white-clubbed' form was first obtained from *G. morsitans*, in Nyasaland (Waterston, 1916), and was probably used by Lamborn (1916, 1925) in his field experiments on the biological control of tsetse. The 'white-clubbed' form has also been obtained by the author from *G. morsitans* collected in Tanganyika and from *G. pallidipes* from Kenya.

It may be seen that the distributions of the two forms of *Syntomosphyrum* overlap in Tanganyika (in *G. morsitans*) and Kenya (in *G. pallidipes*). Investigations show that the optimum relative humidity for the survival of the adults is 80–85 per cent., and that a constant temperature of 32.5°C. for 24 hours is lethal to the eggs (Saunders, *in preparation*). For these reasons, the breeding places of these parasites are probably restricted to localised, shaded sites beneath fallen logs and amongst leaf humus, which also afford sites for pupae of *Glossina*. Therefore, in Kenya and Tanganyika (and possibly elsewhere) the two forms of *Syntomosphyrum* probably occur in similar sites and utilise pupae of the same species of *Glossina*.

Dobzhansky (1935) defined species as representing "that stage in the evolutionary process at which the once actually or potentially interbreeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding." The two potentially interbreeding forms considered in the present paper are able to copulate in laboratory experiments, but the females are never fertilised. This is evidence of a physiological barrier between the two forms. Even though they seem to occur in similar microhabitats, they probably never attempt to cross-mate in nature owing to the rarity of parasitised pupae (the natural parasitism of *Glossina* pupae is less than 0.25 per cent.) and the likely prevalence of sib matings between the progeny of a single host. The two populations of the 'dark-clubbed' form, from Kenya and Nigeria, although separated geographically by almost a continent, were able, when brought together, to produce fertilised eggs. The evidence as a whole suggests that the two populations of 'dark-clubbed' *Syntomosphyrum* represent the same species (*S. glossinae* Wtstn.) and that the 'white-clubbed' form is a separate species.

Summary.

Cross-mating experiments are reported between adults of the typical, dark-clubbed form of *Syntomosphyrum glossinae* Wtstn., obtained from pupae of *Glossina pallidipes* Aust. from Kenya and of *G. palpalis* (R.-D.) and *G. morsitans submorsitans* Newst. from Northern Nigeria, and the 'white-clubbed' form of *Syntomosphyrum*, originally reported by Waterston from Nyasaland, obtained from pupae of *G. morsitans* Westw. from Tanganyika.

Fertilised eggs, giving rise to offspring of both sexes, were produced only by crosses between the strains of typical *S. glossinae*. Crosses in either direction between the 'white-clubbed' form and typical *S. glossinae* resulted in all-male progeny, presumed to develop from unfertilised eggs. It is considered that this is evidence of a physiological barrier to reproduction between the two forms. The 'white-clubbed' form is therefore regarded as a distinct species.

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References.

- DOBZHANSKY, T. (1935). *Drosophila miranda*, a new species.—*Genetics* **20** pp. 377-391.
- LAMBORN, W. A. (1916). Third report on *Glossina* investigations in Nyasaland.—*Bull. ent. Res.* **7** pp. 29-50.
- LAMBORN, W. A. (1925). An attempt to control *Glossina morsitans* by means of *Syntomosphyrum glossinae*, Waterston.—*Bull. ent. Res.* **15** pp. 303-309.
- NASH, T. A. M. (1933). The ecology of *Glossina morsitans*, Westw., and two possible methods for its destruction. Part II.—*Bull. ent. Res.* **24** pp. 163-195.
- TORVIK-GREB, M. (1935). The chromosomes of *Habrobracon*.—*Biol. Bull., Wood's Hole* **63** pp. 25-34.
- VANDEL, A (1931). La parthénogenèse.—*Encycl. sci., Bibl. Biol. gén.*, 412 pp. Paris, Doin.
- WATERSTON, J. (1915). Notes on African Chalcidoidea. II.—*Bull. ent. Res.* **5** pp. 343-372.
- WATERSTON, J. (1916). Chalcidoidea bred from *Glossina morsitans* in Nyasaland.—*Bull. ent. Res.* **6** pp. 381-393.

THE FORMS OF *SYNTOMOSPHYRUM* (HYM., EULOPHIDAE) PARASITIC ON TSETSE FLIES.

By G. J. KERRICH

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The taxonomic problem.

Two forms of *Syntomosphyrum* parasitic on tsetse flies (*Glossina* spp.) are known. Waterston (1915) described the first, in which the female has the antennal club, like the funicle, wholly fuscous, as a new species, *Syntomosphyrum glossinae*. His description was made from a comparatively short series of specimens, most of which have the antennae broken; but from the female holotype it is confirmed that it was indeed the fuscous-clubbed form that was described.

In a slightly later paper (1916), Waterston described the second form, which was from a different locality and host species, as an infra-specific form without defined status: "In these Nyasaland *S. glossinae* the coloration is richer than in the type, the pedicel and funicular joints being dark and the club as a rule entirely pale." He gave no indication as to whether he had attempted to distinguish this 'Nyasaland form' in any other way from the fuscous-clubbed form, which he had described in considerable detail, as was his custom when validating new species.

In response to a request from Dr. D. S. Saunders, who was making biological studies on the 'white-clubbed' form, I subjected the two forms to intensive museum study, but found that most differences that seemed at first sight to separate them, other than the colour of the female antennal club, appeared to break down.

Dr. B. D. Burks, of the U.S. Department of Agriculture, Washington, D.C., was then so kind as to examine long series of specimens of both forms. He largely confirmed my negative findings but was able to point out the manner in which a suggested slight difference in the proportions of the antennal funicles could be made susceptible to definition.

In the majority of series, this characterisation can be supported by a difference in general body colour, particularly on the frontovertex and prescutum, but such difference must be used with the greatest caution. In general, the 'white-clubbed' form has the parts mentioned bluish-green, the fuscous-clubbed form greenish-blue; but one colleague, examining female paratypes with broken antennae, thought to place them with the 'white-clubbed' series upon this colour difference. The colour appearance is affected by the illumination. On 4th November 1959, I examined the holotype of *glossinae*, illuminated with a spotlight and good daylight and found it to be green; but the appearance had changed to blue by 3.20 p.m. when daylight had largely faded.

Neither Dr. Burks nor I succeeded in finding a morphological separation for the males.

Saunders (1960) has found that the two forms are not inter-fertile under laboratory conditions. Although the known range of the fuscous-clubbed form extends into moist, forested areas and the 'white-clubbed' form is known only from dry savannah country, there has been found to be overlap in both territory and host species. Accordingly, I designate the 'white-clubbed' form as a sibling species rather than as an infra-specific form.

Here I have a correction to make to Waterston's statement that the eyes are

bare, but that under high magnification ($\times 600$) one or two minute scattered hairs may be detected. This observation was evidently made from a slide mount of a potashed specimen from which nearly all the hairs had been loosened. From an examination of card-pointed specimens, including the holotype of *glossinae*, I find that in both species the eyes are rather densely hairy, discernibly so at $\times 65$ and quite distinctly at $\times 100$.

Validation of the 'white-clubbed' species.

Syntomosphyrum albi clavus, sp.n.

Female: length 1.3 to 1.7 mm. Structurally similar to *glossinae* except in the proportion of the antennal segments. First and second funicle segments almost equal in length, the second slightly the wider; third funicle slightly shorter than, but equal in width to, the second; club as long as first and second funicles and slightly wider than second.

Head and dorsum of thorax and propodeum blue-green, with bright metallic reflections, the green more intense on frontovertex and prescutum than elsewhere: sides and venter of thorax and sides of propodeum black, or paler, with metallic reflections or lustre: mandibles a rich brown, black at apex: antennae with scape pale yellow, with pedicellus darkish brown above but paler below, with funicle segments darkish brown and with club white, darkened only at base: tegulae and wing veins pale yellow, the latter rather duller, forewing shaded with brown, hindwing hyaline: legs pale yellow, or the fore coxae and trochanters more whitish, the tarsi blackened only at extreme apex: the minute petiolar segment whitish: remainder of gaster tan coloured above, rather paler below, blackened more or less broadly at apex and sides, and with more or less definite infusate bands above, the front angles shining green.

Holotype ♀ in British Museum (Natural History), a specimen selected from the series from Nyasaland, Lake Nyasa, Monkey Bay, 17.vi.1915, *ex Glossina morsitans* Westw. (*W. A. Lamborn*) described by Waterston (1916) as the 'Nyasaland form' of *S. glossinae*. Other material in British Museum (Natural History), U.S. National Museum, and London School of Hygiene and Tropical Medicine.

Key to species of *Syntomosphyrum* parasitic on tsetse flies (*Glossina* spp.): females.

Antenna with first funicle segment about one-fifth longer than second; with funicle and club a darkish brown, the club somewhat paler at apex but not white: head and thorax, notably the frontovertex and prescutum, usually decidedly a greenish-blue, the frontovertex often indigo, appearing greenish only in parts as viewed very obliquely; but sometimes more green, often with rather strong bronzy reflections *glossinae* Waterston.

Antenna with first funicle segment not or very little longer than second; with funicle darkish brown but club white, darkened only at base: head and thorax, notably the frontovertex and prescutum, decidedly a bluish-green
albi clavus, sp.n.

Summary of material seen.

Syntomosphyrum glossinae: UGANDA: Victoria Nyanza, Wema Is., 7 ♀♀, 2 ♂♂, *ex G. palpalis* (R.-D.) (type series) (*G. D. Hale Carpenter*); TANGANYIKA: unlocalised and undated (but presented to B.M. 1933), 12 ♀♀ *ex G. morsitans* (*T. A. M. Nash*); NYASALAND: Fort Johnston, reared on *Dacus* as laboratory host, vi.1922, numerous ♀♀ ♂♂ (ref. 515) (*W. A. Lamborn*); NYASALAND: Fort Johnston, reared on laboratory host, 11 ♀♀, 7-9.viii.1928 (*W. A. Lamborn*);

KENYA: South Kavirondo, Lambwe Valley, 11 ♀♀, 4 ♂♂, viii.1937, *ex G. pallidipes* Aust. (*E. A. Lewis*); NIGERIA: Kaduna, 14.iv.1947, 5 ♀♀, 3 ♂♂ *ex G. palpalis* (*T. A. M. Nash*); LIBERIA: R. Bola, Kaia, 4 ♀♀ *ex G. palpalis* 1944 (*J. Bequaert*) (U.S. National Museum); KENYA: Makueni, numerous ♀♀ ♂♂, 1958, stock *ex G. pallidipes* (*per D. S. Saunders*); NIGERIA: Kaduna, fuscous-tip associated ♂♂, 1958, stock *ex G. pallidipes* (*per D. S. Saunders*); TANGANYIKA: 1948, 9 ♀♀, 1 ♂, *ex G. morsitans* (London School of Hygiene & Tropical Medicine).

Syntomosphyrum albiclavus, sp.n.: NYASALAND: Lake Nyasa, Monkey Bay, 10 ♀♀ (out of 13 recorded), 17.vi.1915, *ex G. morsitans* (*W. A. Lamborn*); NYASALAND: Lake Nyasa, Monkey Bay, numerous specimens in British Museum, 27.vii.–6.viii.1915, *ex G. morsitans*; NYASALAND: Fort Johnston, reared on various laboratory hosts, 1922, numerous specimens in British Museum (*W. A. Lamborn*); NORTHERN RHODESIA: Ngoa, 9 ♀♀, 1 ♂, 23.ix.–27.x.1915, *ex G. morsitans* (*Ll. Lloyd*); TANGANYIKA: Singida, numerous ♀♀ ♂♂, 1958, stock *ex G. morsitans* (*per D. S. Saunders*).

Summary.

The object of this paper is to give taxonomic consideration and status to the 'white-clubbed' parasite of tsetse flies that was studied by Dr. D. S. Saunders in the foregoing paper. Since the biological evidence in conjunction with the distribution suggests that it is specifically distinct from *Syntomosphyrum glossinae* Waterston it is described as a new species, although the morphological separation is weak.

Acknowledgements.

The author wishes to thank Dr. B. D. Burks of the U.S. Department of Agriculture, Washington, D.C., for his help in solving this difficult problem.

References.

- SAUNDERS, D. S. (1960). The 'white-clubbed' form of *Syntomosphyrum* (Hym., Eulophidae) parasitic on tsetse flies.—*Bull. ent. Res.* **51** pp. 17–20.
 WATERSTON, J. (1915). Notes on African Chalcidoidea. II.—*Bull. ent. Res.* **5** pp. 343–372.
 WATERSTON, J. (1916). Chalcidoidea bred from *Glossina morsitans* in Nyasaland.—*Bull. ent. Res.* **6** pp. 381–393.

ON THE STAGES IN THE DEVELOPMENT OF *SYNTOMOSPHYRUM*
ALBICLAVUS KERRICH (HYM., EULOPHIDAE), A PARASITE
 OF TSETSE FLIES.

By D. S. SAUNDERS *

Department of Entomology, London School of Hygiene
 and Tropical Medicine.

Pl.

(PLATE III.)

Two species of *Syntomosphyrum* (*S. glossinae* Wtstn. and *S. albiclavus* Kerrich) have been recorded as parasites of pupae of *Glossina*. *S. glossinae* was first discovered by Fiske, in Uganda, in 1913, when specimens emerged from parasitised pupae of *G. palpalis* (R.-D.) collected on Wema Island, Lake Victoria (in Fiske, 1920); the species was described by Waterston (1915). *S. albiclavus* was first recorded, as a variant of *S. glossinae*, by Waterston (1916) from pupae of *G. morsitans* Westw. collected in Nyasaland, but not recognised as a separate species (Kerrich, 1960) until biological evidence to that effect was produced by Saunders (1960). Consequently, the literature refers only to *S. glossinae* and gives little indication of the species concerned.

The two species of *Syntomosphyrum* have a high rate of increase and can easily be bred in blowfly pupae in the laboratory (Lamborn, 1925, Nash, 1933). For these reasons the parasites seemed to present a means for biological control of the tsetse fly. In this connection four field experiments were conducted—three in East Africa (Lamborn, 1925, Nash, 1933, Lloyd, H. M. (in Swynnerton, 1936)) and one in Nigeria (Lloyd, Johnson & Rawson, 1927). All these experiments, however, proved unsuccessful. During them a good deal of information was collected on the methods of breeding and liberation of these parasites. On the other hand, very few laboratory studies of these parasites have been carried out and up till now no one has described the immature stages.

The immature stages of several other Eulophids have, however, been studied, for example: *Dahlbominus* (cited as *Microplectron*) *fuscipennis* (Zett.), a parasite of sawflies of the genus *Diprion* in eastern Europe, was investigated by Morris & Cameron (1935); *Chrysocharis gemma* (Wlk.), *C. syma* (Wlk.) and *Pediobius* (cited as *Pleurotropis*) *amyntas* (Wlk.), parasites of the holly leaf-miner, *Phytomyza ilicis* Curt., by Cameron (1939); and *Tetrastichus hagenowii* (Ratz.), a parasite of cockroach oothecae, by the same author (Cameron, 1955). The present paper is a description of the immature stages of *S. albiclavus*.

Materials and methods.

The present study is based on material of *S. albiclavus* that emerged from pupae of *G. morsitans* collected near Singida, Tanganyika. The great practical difficulties involved in maintaining a laboratory supply of tsetse-fly pupae were avoided by breeding the parasites in pupae of *Lucilia sericata* (Mg.), which is easily maintained in captivity. Day-old pupae were exposed to the parasite for six hours and then incubated at 25°C. in 3 in. × 1 in. specimen tubes. This procedure was repeated daily with fresh pupae, thus providing a continuous

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supply of parasites. The immature stages of the parasite were then removed from the host pupae when required, and mounted for microscopical examination.

The immature stages of *Syntomosphyrum albiclavus*.

Eggs.

The mature female of *Syntomosphyrum* drills through the puparium of a selected host with her ovipositor (see Plate III, figs. 1 & 2) and deposits the eggs on the surface of the pupa; the subsequent immature stages live in the space between the pupa and the puparium.

Each egg is approximately 0.42 mm. long and 0.06 mm. at its widest (fig. 1, B); it is translucent when first laid, but later becomes opaque. At 25°C., the egg hatches about 48 hours after oviposition. The number of eggs laid in a batch varies considerably, depending on the size and age of the female. Under favourable conditions a batch may consist of 40 to 50 eggs. If a pupa is attacked by a parasite that is immature, no eggs are laid, and a parasite that is nearing the end of its laying life may not lay on the pupa it has attacked. In such cases, the development of the host ceases, showing that it has been killed or paralysed by the parasite. The contents of such a pupa remain suitable for *Syntomosphyrum* until decomposition sets in, and will support larvae resulting from subsequent attacks by the parasite. In this connection it is of interest to note that Lamborn (1925) reared up to three consecutive broods of *Syntomosphyrum* from a single blowfly pupa.

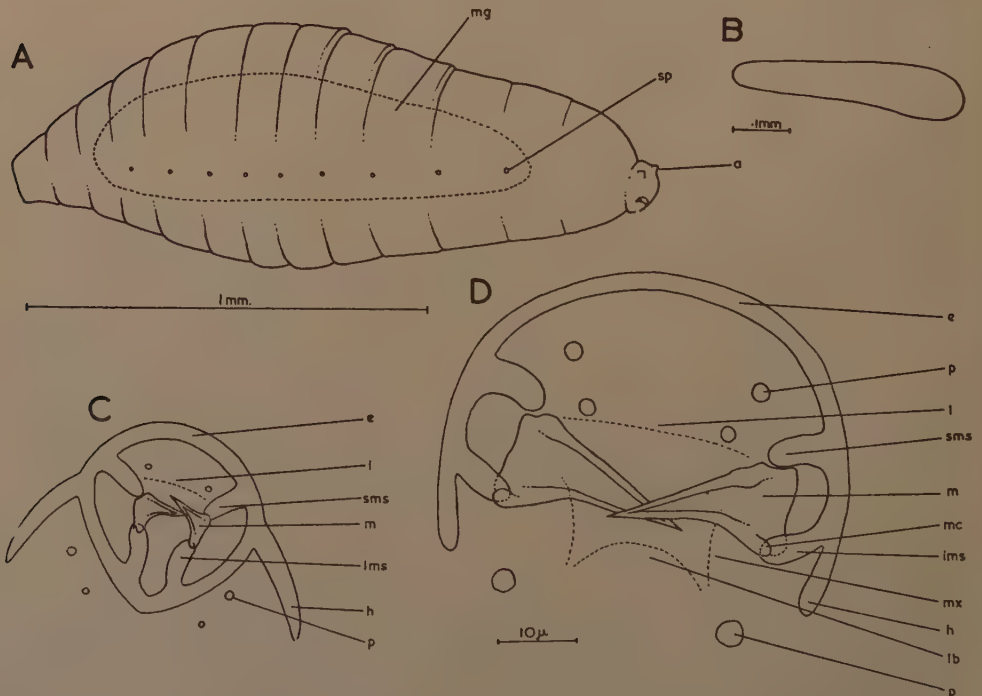


Fig. 1.—*Syntomosphyrum albiclavus*. A, fourth-instar larva (side view); B, egg; C, cephalic skeleton of first-instar larva; D, cephalic skeleton of fourth-instar larva. a, antenna; e, epistome; h, hypostome; lms, inferior mandibular strut; l, labrum; lb, labium; m, mandible; mc, mandibular condyle; mg, mid-gut; mx, maxilla; p, papilla; sms, superior mandibular strut; sp, spiracle.

Larvae.

The larvae are translucent and apodous with a head and 13 body segments (fig. 1, A and Plate III, fig. 3). The antennae are minute and a series of papillae are present on the labrum and labium. The only sclerotised structures in the larva are the mandibles and the associated cephalic skeleton, the latter consisting of a series of cuticular bars supporting the mandibles. The mandibles are spine-like and articulate with two pairs of condyles.

The arrangement of the apodemes of the cephalic skeleton in the primary larva differs from that in the mature larva. In the case of the first-instar larva the inferior mandibular struts are fused behind the mouth and the hypostomal elements are splayed laterally, but in the subsequent instars the inferior mandibular struts are not joined behind the mouth and the hypostomal elements are in a continuous arc with the epistome (fig. 1, C and D). The tentorium, which is well developed in the larvae of the Pteromalid, *Mormoniella vitripennis* (Wlk.), and the Eulophid, *Dahlbominus fuscipennis* (Morris & Cameron, 1935), seems to be absent in *Syntomosphyrum*.

In the larvae of *S. albiclavus* the tracheal system is well developed and there are two pairs of thoracic and seven pairs of abdominal spiracles. When the larva is mounted in Gater's fluid, air remains in the tracheae until the process of clearing is complete, showing the presence of two lateral tracheal trunks and many side ramifications. The salivary ducts may also be seen in these freshly mounted larvae, opening into the mouth just dorsal to the labium.

One of the objects in the present investigation was to discover the number of larval instars in the development of *S. albiclavus*. This was done by the application of Dyar's law to measurements of the width of the cephalic skeleton. To do this, larvae of all ages were removed from their hosts and mounted with their ventral sides uppermost in polyvinyl-lactophenol containing a small amount

TABLE I.

Application of Dyar's law to determine the number of larval instars in *S. albiclavus*.

Days after oviposition	Number of measurements	Mean width of cephalic skeleton (microns)	Range of width (microns)	Instar number
3	25	26.5	25.0-28.0	1
4	23	40.6	37.4-42.5	2
5	18	61.9	59.5-65.0	3
6-10	51	91.5	85.0-95.2	4

Calculation of geometrical progression :

$$\frac{\text{Instar 2}}{\text{Instar 1}} = \frac{40.6}{26.5} = 1.53$$

$$\frac{\text{Instar 3}}{\text{Instar 2}} = \frac{61.9}{40.1} = 1.52$$

$$\frac{\text{Instar 4}}{\text{Instar 3}} = \frac{91.5}{61.9} = 1.48$$

Mean progression, 1.51

of lignin pink. This mountant served to fix and clear the larvae and also to stain the sclerotised structures of the head. The width of the cephalic skeleton at its widest point (opposite the inferior mandibular struts) was then measured by means of a calibrated eyepiece micrometer. In the primary larva, the distance measured was the width of the cephalic ring minus the laterally splayed hypostomal elements. The measurements thus obtained were found to fall into four groups, each presumably corresponding to an instar. According to Dyar (1890), who worked on Lepidopterous larvae, the width of the head capsule, which does not change during a stadium, increases at each ecdysis in a regular geometrical progression. By dividing the width of the head capsule in one instar by the width of the head capsule in the preceding one it is therefore possible to see whether an instar has been overlooked. Cameron (1934) applied a similar technique to the larval exuviae of *Haematopota pluvialis* (L.), in which he measured the combined length of the mandibles and the cephalic tentorial rods. On the other hand, in some species of insect, such as *Popillia japonica* Newm., there is no regular progression between the measurements of thickly sclerotised parts, and Dyar's law cannot be applied (Abercrombie, 1936). The application of this calculation to the widths of the cephalic skeleton in *S. albiclavus*, however, shows the progression to be sufficiently regular to suggest that no instars have been missed (Table I). This, together with the facts that the youngest larvae were found in the same batch as hatching eggs and the oldest with prepupae, demonstrates that there are four larval instars. Other observations that corroborate this conclusion are that both second-instar larvae and pupae were found in the process of ecdysis, shedding the pellicle of the preceding instar together with its mouthparts. If instar number is plotted against the logarithm of the observed width of the cephalic skeleton, a straight line results (fig. 2). It is of

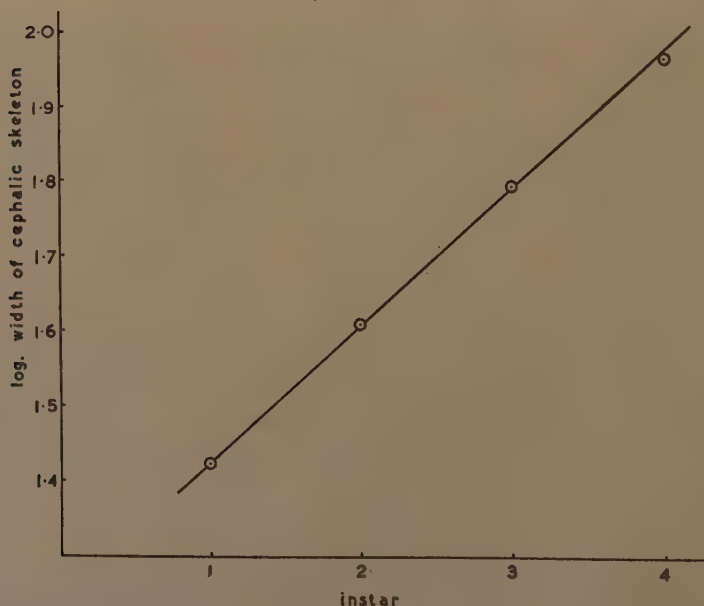


Fig. 2.—Instar number plotted against logarithm of observed width of cephalic skeleton of larvae of *Syntomosphyrum albiclavus*, illustrating Dyar's law.

interest to note that Morris & Cameron (1935) found another species of Eulophid, *Dahlbominus fuscipennis*, to have five larval instars.

At 25°C. the duration of each of the first three larval stages is about 24 hours, and of the fourth, about five days. When fully fed, the last-instar larvae arrange themselves within the host puparium in an upright position. Defaecation then occurs and they assume the prepupal form, which is recognised by the lack of faecal material in the gut and the differentiation of the body into thoracic and abdominal regions (fig. 3, A). The prepupae then change into pupae. This stage in the metamorphosis is slow, and at 25°C. takes about 48 hours. At first, the pupae remain in an unexpanded condition and are still covered by the last larval skin, complete with larval mouthparts (fig. 3, B). Eventually the larval skin is shed and the pupae are fully formed (fig. 3, C), attached by their posterior ends to a pad of unconsumed host material and larval exuviae.

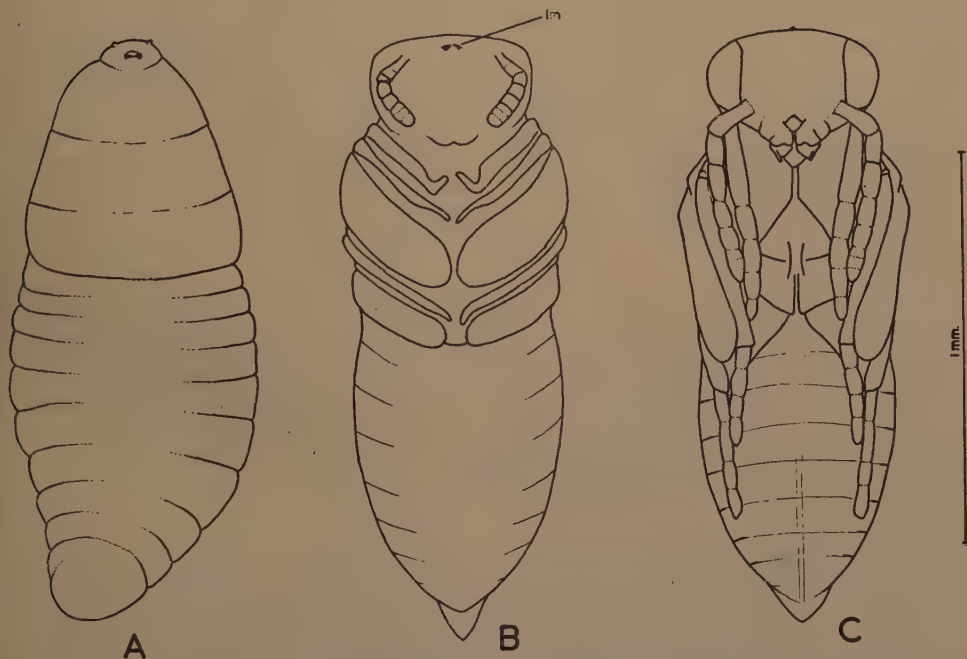


Fig. 3.—*Syntomosphyrum albiclavus*. A, prepupa; B, unexpanded pupa, still covered by the last larval skin; C, pupa. lm, larval mandibles.

Pupae.

As in most Chalcidoids, the pupa is exarate and without a cocoon (Pl. III, fig. 4). It is uniformly white in colour, but after a few hours the compound eyes and ocelli have become bright red. After a few days, the coloration of the adult integument develops, first in the head and thorax and later in the abdomen, until the adult is ready to emerge. The duration of the pupal stage at 25°C. is about ten days. After the adults emerge they remain within the host puparium for about 24 hours. The adult parasites then bite a small emergence hole in the puparium and escape. Both sexes are capable of biting this hole, although it is generally done by the females, which are normally present in greater numbers. Copulation occurs within a few moments of emergence from the host, and the females are mature in about three days and able to parasitise new pupae.

Discussion.

Since the demonstration by Dyar (1890) that the width of the head capsule in successive instars of a Lepidopterous larva increased in a regular geometrical progression, it has been shown, in many insects, that measurements of other parts of the body increase in a similar fashion. On the other hand, there are exceptions to this rule. Richards (1949) showed that measurements such as the width of the insect head capsule only increases regularly if all the instars are of the same duration. He pointed out that growth in insects proceeds at a regular rate, although expansion of those parts of the body bounded by a rigid integument only occurs immediately after ecdysis, and that expansion of these sclerotised structures is therefore greater after a stage of long duration than after one of short duration. The fourth larval stage in the life-cycle of *S. albiclavus* is the longest, but this does not affect the application of Dyar's law to *Syntomosphyrum*, because at ecdysis the fourth-instar larva becomes the pupa, which has a different form and is therefore not included in the calculation.

In the course of this work it was observed that the size of *S. albiclavus* depends on a nutritional factor associated with the number of larvae developing on a host pupa. If overcrowded, the resultant adult parasites are small. It might be expected, therefore, that overcrowding would affect the size of the cephalic skeleton and hence the application of Dyar's rule. The effects of overcrowding, however, do not become apparent until the fourth larval instar, the width of the cephalic skeleton of which has already been determined and is the last to enter into the calculation of Dyar's rule, the application of which is accordingly not affected by overcrowding.

Summary.

The life-cycle and immature stages of the Eulophid, *Syntomosphyrum albiclavus* Kerrich, a pupal parasite of tsetse flies (*Glossina*), are described. Measurements of the widths of the cephalic skeletons of larvae of all ages fell into four well separated groups, and confirmation that these represented the existence of four larval instars was given by Dyar's law, the application of which in this instance is not invalidated by the disproportionate length of the fourth instar or the effects of overcrowding, which do not become apparent before that stage.

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References.

- ABERCROMBIE, W. F. (1936). Studies on cell number and the progression factor in the growth of Japanese beetle larvae (*Popillia japonica* Newman).—*J. Morph.* **59** pp. 91–112.

- CAMERON, A. E. (1934). The life-history and structure of *Haematopota pluvialis*, Linné (Tabanidae).—*Trans. roy. Soc. Edinb.* **58** pp. 211–250.
- CAMERON, E. (1939). The holly leaf-miner (*Phytomyza ilicis*, Curt.) and its parasites.—*Bull. ent. Res.* **30** pp. 173–208.
- CAMERON, E. (1955). On the parasites and predators of the cockroach. I. *Tetrastichus hagenowii* (Rätz).—*Bull. ent. Res.* **46** pp. 137–147.
- DYAR, H. G. (1890). The number of molts of Lepidopterous larvae.—*Psyche* **5** pp. 420–422.
- FISKE, W. F. (1920). Investigations into the bionomics of *Glossina palpalis*.—*Bull. ent. Res.* **10** pp. 347–463.
- KERRICH, G. J. (1960). The forms of *Syntomosphyrum* (Hym., Eulophidae) parasitic on tsetse flies.—*Bull. ent. Res.* **51** pp. 21–23.
- LAMBORN, W. A. (1925). An attempt to control *Glossina morsitans* by means of *Syntomosphyrum glossinae*, Waterston.—*Bull. ent. Res.* **15** pp. 303–309.
- LLOYD, LL., JOHNSON, W. B. & RAWSON, P. H. (1927). Experiments in the control of tsetse-fly. (Report of the tsetse investigators in N. Nigeria).—*Bull. ent. Res.* **17** pp. 423–455.
- MORRIS, K. R. S. & CAMERON, E. (1935). The biology of *Microplectron fuscipennis*, Zett. (Chalcid.), a parasite of the pine sawfly (*Diprion sertifer*, Geoff.).—*Bull. ent. Res.* **26** pp. 407–418.
- NASH, T. A. M. (1933). The ecology of *Glossina morsitans*, Westw., and two possible methods for its destruction. Part II.—*Bull. ent. Res.* **24** pp. 163–195.
- RICHARDS, O. W. (1949). The relation between measurements of the successive instars of insects.—*Proc. R. ent. Soc. Lond. (A)* **24** pp. 8–10.
- SAUNDERS, D. S. (1960). The 'white-clubbed' form of *Syntomosphyrum* (Hym., Eulophidae) parasitic on tsetse flies.—*Bull. ent. Res.* **51** pp. 17–20.
- SWYNNERTON, C. F. M. (1936). The tsetse flies of East Africa. A first study of their ecology, with a view to their control.—*Trans. R. ent. Soc. Lond.* **84** pp. 1–579.
- WATERSTON, J. (1915). Notes on African Chalcidoidea. II.—*Bull. ent. Res.* **5** pp. 343–372.
- WATERSTON, J. (1916). Chalcidoidea bred from *Glossina morsitans* in Nyasaland.—*Bull. ent. Res.* **6** pp. 381–393.

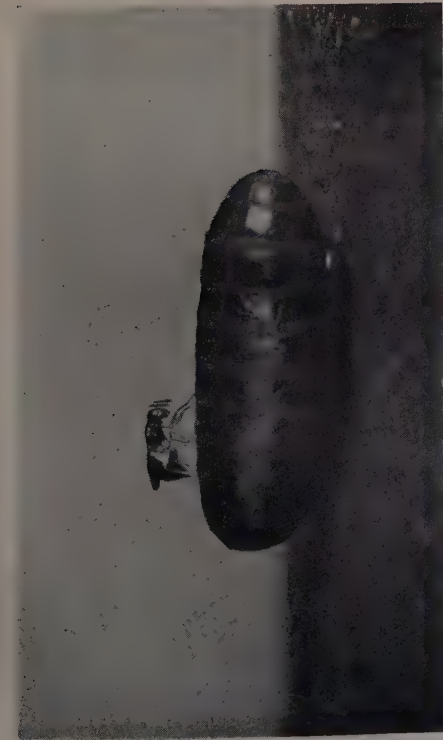


FIG. 1. *Syntomosphyrum albiclavus*: female drilling in a puparium of *Lucilia sericata*.



FIG. 2. *S. albiclavus*: female drilling in a puparium of *L. sericata*, with ovipositor fully inserted.



FIG. 3. Puparium of *L. sericata* opened to show fully fed larvae of *S. albiclavus*.



FIG. 4. Puparium of *L. sericata* opened to show pupae of *S. albiclavus*.

THE MEASUREMENT OF SIZE IN TSETSE FLIES (*GLOSSINA*).

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One of the most important requisites for physiological studies is a convenient and accurate measure of size; without it, differences in rates of physiological processes or in quantities of food and water reserves cannot reliably be corrected for differences in size between individuals or samples studied. In tsetse flies (*Glossina*), residual dry weight (= dry weight minus fat) has proved adequate in this respect as far as the extruded larva, the pupa and the teneral (*i.e.*, unfed) fly is concerned, because it remains nearly constant throughout this period of development and until near the end of teneral life. But it cannot be used for flies that have taken their first blood-meal, because the blood-meal itself contributes so largely to the residual dry weight of the whole fly, which consequently undergoes extensive variations in the course of each hunger cycle. To find a measure of size that remains constant throughout the life of such flies it is necessary to resort to linear measurements. One such, which has been in use for many years, is the length of the middle part of the fourth longitudinal wing vein (Jackson, 1946). This measure suffers from the disadvantage that the wing has to be removed and mounted before the measurement can be made; but more serious is the fact that it is poorly correlated with the residual dry weight of unfed flies, so that estimates of size based on small samples may be highly inaccurate. Attempts have therefore been made to find a more satisfactory measure of size.

Results.

Much of the work for which a measure of size had to be obtained was concerned with rates of transpiration and respiration, and in view of the 'surface effect' that is considered to be operative in such rate-processes (see, for example, Edwards, *in* Roeder, 1953) it was thought desirable to employ a measure of surface rather than of length or breadth. A number of different dimensions were tried, and the one finally adopted as being relatively convenient to measure, constant throughout adult life and closely correlated with residual dry weight in teneral flies, was a function of the dorsal thoracic surface; more precisely, it was the product of the distance between the points of insertion of the largest of the lateral pronotal spines and of the distance between the base of the scutellar spines and the mesonotal suture. The distances were measured under a low-power objective with a micrometer eyepiece, the fly being mounted on an upright pin thus enabling correct alignment in relation to the optical system. This measure of surface was subsequently found unsuitable for work on transpiration (Bursell, 1959) but it has been used to advantage in several other studies and is therefore described here in some detail.

The close correlation between dorsal thoracic surface and residual dry weight is shown in fig. 1 for females of *G. morsitans* Westw. bred in the laboratory from puparia maintained at 28°C. The wing-vein length of these same females (mean of right and left wings) is shown in the same figure, and the relation is obviously

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far less close. The coefficients of correlation between thoracic surface and residual dry weight for the females and for a batch of 8 males similarly maintained were 0.9671 and 0.8815, respectively. The corresponding values for wing-vein length were 0.8007 and 0.6701; even with these small samples the difference is significant at the 5 per cent. level when the coefficients for the two sexes were summed by z-transformation.

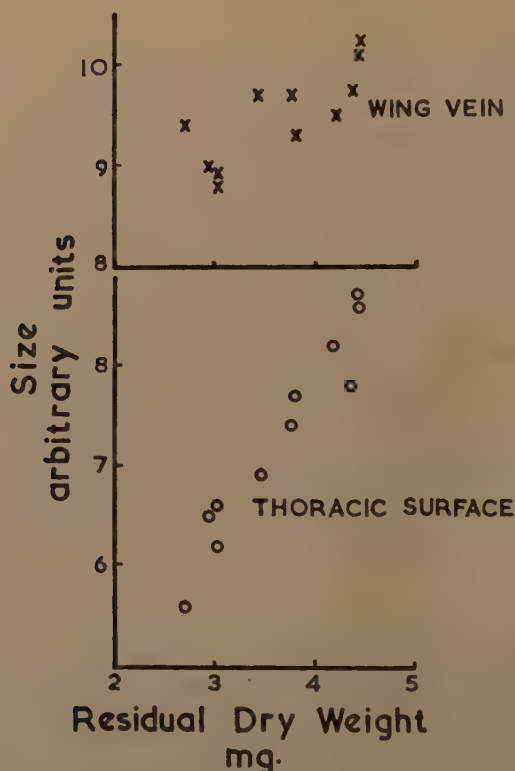


Fig. 1.—The wing-vein length and the dorsal thoracic surface of females of *G. morsitans* plotted as a function of their residual dry weight. The flies were bred in the laboratory from puparia maintained at 28°C.

Further work has shown that both these measures of size, and probably other linear dimensions as well, are subject to one major disadvantage, namely that they are affected by the temperature at which the pupal development takes place. The dorsal thoracic surface of flies having a residual dry weight of 3.60 mg. (calculated by regression*) is shown in fig. 2 as a function of the temperature obtaining during pupal development. Females are about 13 per cent. bigger than males of the same residual dry weight, so in order to represent both sexes on a single curve the female ordinate has been displaced by an amount cor-

* Regressions were calculated of surface on residual dry weight for each sex at each temperature and comparisons made at the specified level of residual dry weight.

responding to the mean difference between the sexes, weighted by the reciprocal of the variance at each temperature. It is clear that above a temperature of about 25°C. the extent of the thoracic surface decreases quite sharply in flies of any given residual dry weight, and there appears to be a less pronounced decrease towards lower extremes of the temperature range.

It has been shown that the relation between the weight of puparia at the time

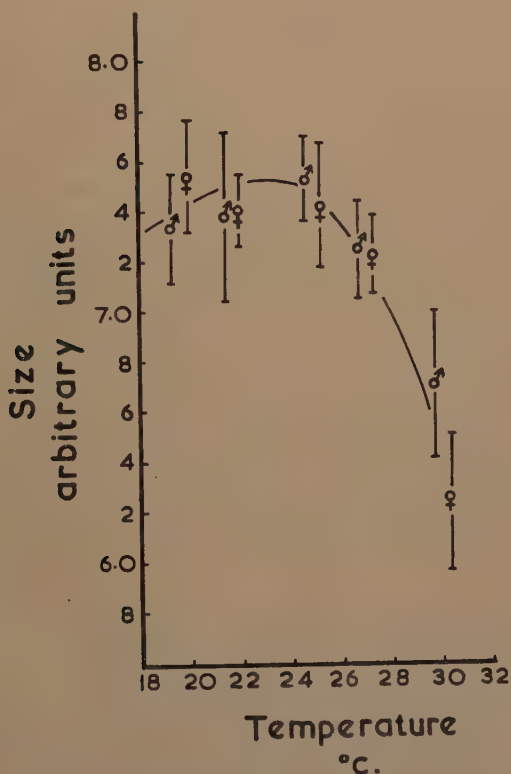


Fig. 2.—The size-specific thoracic surface of *G. morsitans* plotted as a function of the temperature obtaining during pupal development. (See text for further explanation.)

of hardening and darkening and the residual dry weight of emerging flies is independent of temperature (Bursell, The effect of temperature on the consumption of fat during pupal development in *Glossina* †). It appears thus that puparia of a given weight produce smaller but relatively heavier flies at 30 than at 25°C. This has been found to hold good also for *G. pallidipes* Aust. and *G. swynnertoni* Aust. It is contrary to the statement made by Jackson (1953) that the size of tsetse flies, as reflected in wing-vein length, is determined at birth and is unaffected by conditions during pupal development ‡. And it suggests that caution

† To appear in a later part of *Bull. ent. Res.*

‡ Mellanby (1936) was cited in support of this contention, but that author was referring to size as reflected by residual dry weight, and in these terms the statement is valid.

should be exercised in following the implications of this statement, that stresses acting on the pregnant female may be gauged from the size of flies two months later. The range of seasonal change in size reported by Jackson is such that it could theoretically be accounted for by an increase in the temperature of pupal sites from 24 to 30°C. It is unlikely that such a change in temperature would occur in the areas where the work was carried out, and it is not suggested that the results of Jackson's investigations are to be interpreted solely in terms of the effect of temperature during pupal development. But in view of present findings it is clear that, where the mean temperature of pupal sites is likely to exceed 26 or fall below 20°C., detailed inference as to the stresses acting on the pregnant female should be made on the basis of puparial rather than of adult size.

The partial independence of linear dimensions and weight demonstrated by present results is a serious drawback to the use of such dimensions as a measure of size. For unless the object of investigation, for instance transpiration, is causally related to surface rather than to weight it would be misleading to express it in terms of surface; a fly might then have a higher transpiration rate per unit of surface simply because exposure to high temperatures during pupal life had reduced its surface in relation to its weight. A situation of this kind has in fact been reported elsewhere (Bursell, 1959). But since weight cannot be used as a measure of size in non-teneral flies this is a complication which cannot be avoided; if its existence is borne in mind, however, it should be possible to guard against any errors of interpretation that might be caused by it.

The present results are of relevance also to the general problem of the relation between size and the rate of physiological processes, a problem which has been widely discussed in the recent literature (see, for example, Zeuthen, 1953; Ellenby & Evans, 1956; Edwards, 1958), for the possibility of dissociating changes in body surface from changes in weight might provide an important tool for studying the causal mechanisms that underlie such relations; and without an elucidation of these, progress in this field must continue to be slow.

Summary.

A convenient and accurate measure of size is necessary for studies on the physiology of tsetse flies (*Glossina*). Residual dry weight (*i.e.*, dry weight minus fat) is adequate as regards the larva, pupa and teneral fly, but cannot be used for flies that have taken their first blood-meals. A linear measurement provides an index of size that remains constant throughout the life of the fly, but the use of the length of the middle part of the fourth longitudinal vein in the wing has certain disadvantages, and a measure of surface was thought preferable. That finally adopted was a function of the dorsal thoracic surface; details of it are given and a close correlation was demonstrated between it and residual dry weight for females of *G. morsitans* Westw. bred in the laboratory from puparia maintained at 28°C.

The relation between this measure and the weight of the newly emerged fly is affected by the temperature at which the pupal stage is passed; above approximately 25°C. the surface area of flies of any given residual dry weight decreases quite sharply, so that puparia of a given weight produce smaller but relatively heavier flies at 30 than at 25°C. This holds good also for *G. pallidipes* Aust. and *G. swynnertoni* Aust. The dependence of surface area on the temperature at which development has taken place unavoidably complicates the use of this measurement in work on transpiration; it also limits the application of the theory that stresses acting on the pregnant fly may be gauged from the size of flies two months later, and suggests that where the mean temperature of pupal sites is likely to exceed 26°C., any inference should be based on puparial rather than adult size.

References.

- BURSELL, E. (1959). The water balance of tsetse flies.—*Trans. R. ent. Soc. Lond.* **111** pp. 205–235.
- EDWARDS, R. W. (1958). The relation of oxygen consumption to body size and to temperature in the larvae of *Chironomus riparius* Meigen.—*J. exp. Biol.* **35** pp. 383–395.
- ELLENBY, C. & EVANS, D. A. (1956). On the relative importance of body weight and surface area measurements for the prediction of the level of oxygen consumption of *Ligia oceanica* L. and prepupae of *Drosophila melanogaster* Meig.—*J. exp. Biol.* **33** pp. 134–141.
- JACKSON, C. H. N. (1946). An artificially isolated generation of tsetse flies (Diptera).—*Bull. ent. Res.* **37** pp. 291–299.
- JACKSON, C. H. N. (1953). Seasonal variations in the mean size of tsetse flies.—*Bull. ent. Res.* **43** pp. 703–706.
- MELLANBY, K. (1936). Experimental work with the tsetse-fly, *Glossina palpalis*, in Uganda.—*Bull. ent. Res.* **27** pp. 611–632.
- ROEDER, K. D. Ed. (1953). Insect physiology.—1100 pp. New York, Wiley; London, Chapman & Hall.
- ZEUTHEN, E. (1953). Oxygen uptake as related to body size in organisms.—*Quart. Rev. Biol.* **28** pp. 1–12.

THE EFFECT OF HUMIDITY AND TEMPERATURE ON THE
EXTENT OF ABDOMINAL PIGMENTATION IN
GLOSSINA PALLIDIPE AUSTEN.

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(PLATE IV.)

In 1953, Dr. E. Burt, then of the East African Trypanosomiasis Research Organization, discovered that if puparia of *G. pallidipes* Aust. were maintained in dry air the emerging flies failed to develop the dark abdominal banding normally characteristic of the species. Conversely, with puparia maintained at high humidities the emerging flies showed intense blackening of the bands. Previous to this discovery, Dr. Burt had made extensive collections of flies from the field, and had noted that there appeared to be a seasonal variation in the colour of *G. pallidipes* collected at Shinyanga, Tanganyika, with pale flies predominating at the end of the hot, dry season (see Jackson, 1954, for a report of this work)†. Unfortunately Dr. Burt was unable to extend these interesting observations before his retirement in 1956, and it became the privilege of the present author to pursue the question a little further in an attempt to systematise the variations occurring under natural conditions and interpret them in terms of laboratory findings. Many details of the problem have still to be elucidated, but the preliminary results were thought to be of sufficient interest to warrant publication.

Material and methods.

Puparia of *G. pallidipes* were obtained from females collected in the field at Shinyanga and maintained in 3 in. × 1 in. glass tubes. The maintenance tubes were inspected daily at 0730 hr. and any puparia recovered were transferred to desiccators and maintained at constant temperature until emergence of the flies, humidity being controlled at the required values with solutions of potassium hydroxide or with calcium chloride. The flies were kept at 25°C. and 60 per cent. R.H. for one day after emergence; they were then allowed to feed on a sheep and returned to the post-emergence conditions for a further two days to allow full development of cuticle pigmentation. The flies were then killed and their abdomens prepared for examination: the abdomen was snipped off as close as possible to the thorax and its last segment cut off; the abdominal contents were expressed on to filter paper by means of a fine glass roller, and the abdomen then dipped briefly in 70 per cent. alcohol to allow subsequent immersion in a saline solution in which it was washed free of adhering blood. Finally the abdominal cuticle was pressed between pieces of filter paper until dry, in which state it was mounted on a glass slide by means of water-soluble glue. Various mounting media were tried initially (canada balsam, polyvinyl alcohol, glycerine, etc.) but all were found to cause progressive decoloration, and the dry mount was finally adopted as combining the advantages of permanence and simplicity.

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† Series of specimens arranged by Dr. Burt so as to illustrate his observations have been incorporated into the collections of the British Museum (Natural History).—Ed.

For comparison with laboratory-bred flies, teneral (*i.e.*, unfed) flies were collected in the field and fed on arrival at the laboratory; their subsequent treatment was as described above.

To obtain a quantitative estimate of the abdominal pigmentation, the bands were regarded as consisting of a number of zones (fig. 1), each carrying a score



Fig. 1.—Diagram to illustrate the abdominal banding of *G. pallidipes* and the method of its estimation.

of 1. Complete pigmentation, as illustrated in Plate IV (a), would give a score of 15; with the abdomen illustrated in Plate IV (b), pigmentation is less complete, darkening occurring in 8 of the zones (*viz.*, 1, 2, 3, 4, 5, 7, 8 and 11), while the abdomen shown in Plate IV (c) would score on only 4 zones (*viz.*, 1, 2, 3 and 4). The photograph illustrates that in addition to differences in the extent of banding there are also differences in the intensity of coloration of the pigmented portions; thus the pigmented part of the 3rd abdominal segment in Plate IV (b) is not as intensely coloured as is the corresponding segment in Plate IV (a). It has not been possible, however, to get a quantitative estimate of these variations, and, in what follows, no account will be taken of such differences in the colour intensity of pigmented parts. The tendency towards variations in the degree of darkening of pigmented parts is far less in females than in males and for this reason most of the work to be described will relate to the former sex,

Results.

The effect of humidity and temperature on the extent of abdominal pigmentation in G. pallidipes.

The relation between the colour of females and relative humidity at a temperature of 25°C. is shown in fig. 2a, each point representing the mean of 8–12 determinations. It is clear that the extent of coloration gives a very sensitive indication of the humidity to which the puparia have been subjected, the values ranging from almost full pigmentation in saturated air to almost complete suppression of pigmentation in dry air. In males, pigmentation is completely suppressed at a relative humidity of 20 per cent., the difference between the sexes becoming progressively smaller at higher humidities.

The effect of temperature on coloration at two different humidities is shown in fig. 2b; in nearly saturated air, temperature appears to have little effect on the extent of banding until it exceeds 28°C., but at still higher levels the extent

of pigmentation decreases quite sharply. At a relative humidity of 40 per cent., the situation is complicated by the fact that saturation deficiency increases with temperature. If account is taken of this, the results are in accord with those obtained at 98 per cent. R.H. For, by comparison with results obtained at constant temperature, it can be shown that the decrease in pigmentation observed

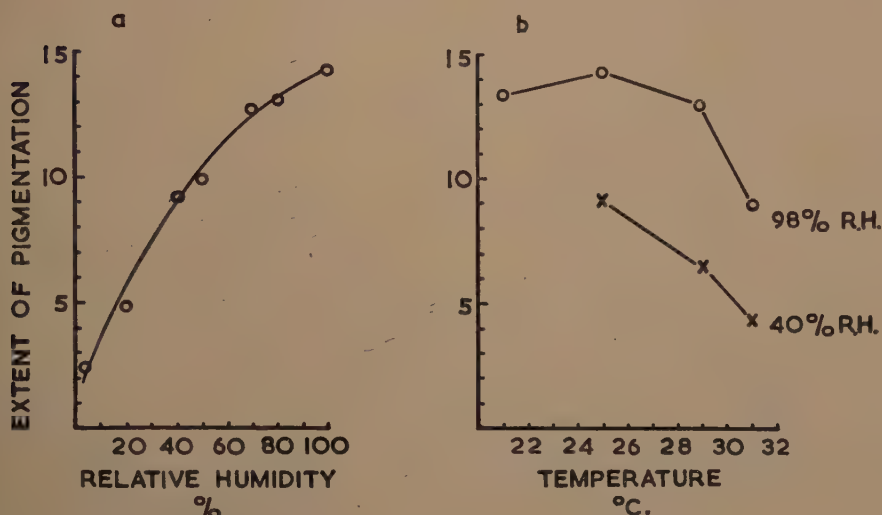


Fig. 2.—a, the effect of different levels of relative humidity at constant temperature (25°C.) on the extent of abdominal pigmentation of females of *G. pallidipes*; b, the effect of different temperatures at constant levels of relative humidity on the extent of abdominal pigmentation of females of *G. pallidipes*.

as the temperature is raised from 25 to 29°C. is adequately accounted for by the increase in saturation deficit, while the further change, when the temperature is raised from 29 to 31°C., is in excess of that which could be expected on the basis of the associated increase in saturation deficiency.

The extent of pigmentation is markedly affected by size. At 40 per cent. R.H., for example, puparia with a mean original weight of 30 mg. produced females with a pigmentation index of 10, while for those with a mean weight of 40 mg. the index was 8. This difference between large and small flies has also been observed in flies collected in the field.

Seasonal changes in the extent of abdominal pigmentation of females of G. pallidipes.

Monthly collections of teneral examples of *G. pallidipes* were made from Block 9, a 50-sq.-mile remnant of tsetse habitat near Shinyanga (for a description of the area, see Vicars-Harris, 1936). The results are presented, as a series of frequency distributions of the different pigment classes, in fig. 3.

Towards the end of the rains (March and April) and at the beginning of the dry season (May) most of the flies fall into the darker pigment categories; as the dry season advances the distribution tends to become bimodal, with the darker mode relatively steady at a pigmentation index of about 12, the paler mode moving progressively down the scale until in October it reaches a pigmentation index of about 5. The pale mode appears to be entirely absent from the November

collection, in which month, the last of the dry season, the dark mode has shifted slightly towards the lighter end of the scale. The first showers occurred in November, and the December and January collections are again unimodal, tending towards the distribution noted in March of the previous year.

In considering the possible interpretation of these changes, it should first be noted that the mean temperature at Shinyanga seldom exceeds 27°C., so that, assuming that the temperature of pupal sites does not differ greatly from mean

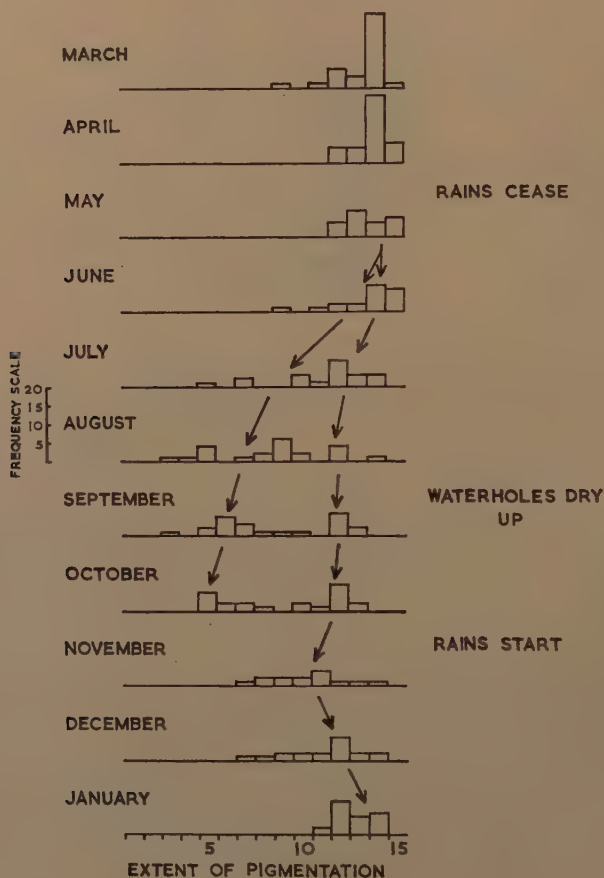


Fig. 3.—Seasonal variations in the extent of abdominal pigmentation (uncorrected) of females of *G. pallidipes* (see text).

shade temperatures (see Bursell, The effect of temperature on the consumption of fat during pupal development in *Glossina* *), the effect of temperature on pigmentation may be ignored and the results interpreted in terms of humidity alone.

Secondly, it is necessary to consider to what extent seasonal fluctuations in size and differences in size between flies bred in the laboratory and in the field may affect the interpretation. In the field, size was constant from March till

* To appear in a later part of *Bull. Ent. Res.*

June, after which it fell progressively to reach a level of 85 per cent. of its peak value in November. At this time, the size was very little different from the mean size of flies bred in the laboratory, and pigmentation may therefore be compared directly with the standard shown in fig. 2a without risk of serious error. Earlier in the year the mean pigmentation indices of samples from the field should be increased by about 1.5 units to allow for the difference in size, this correction factor, which is estimated from regressions of pigmentation on size in laboratory-bred flies, taking intermediate values from July to October.

Bearing in mind these considerations, it seems possible to offer an interpretation of the sequence of events shown in fig. 3 in terms of the observed behaviour of *G. pallidipes* at Shinyanga. The breeding of this species seems to be very widespread during the rainy season (*cf.* Glasgow, 1953, for a preliminary report of Dr. Burt's work in this connection); at this time the soil-space humidity of all pupal sites would be high, giving a predominance of darkly pigmented flies. During the dry season there is a progressive tendency for the flies to concentrate on the evergreen thickets of smaller drainage lines; in August and September, however, gravid females may still be found in isolated thicket clumps on eluvial slopes remote from the drainage lines, and puparia have been recovered from such sites, although puparia are at this time more readily obtained from riverine thickets. It seems not unlikely that the bimodal distribution of pigment classes is a reflection of this use of two types of breeding ground; it may be surmised that the soil-space humidity of pupal sites under semi-deciduous thickets of the eluvial vegetation may be comparatively low, thus giving rise to the paler mode of colour index, the sites becoming progressively drier with the advance of the dry season, and the flies bred there progressively paler. The soil-space humidity of breeding sites in the riverine thickets, on the other hand, seems to change little during the dry season, although there is some indication of a shift in the position of the mode of the sample collected in November. With the advent of early showers in November and of the rains proper in December the breeding population tends to disperse from the riverine thickets, but by that time the humidity of pupal sites has been raised irrespective of the vegetation type, so that the colour distribution returns to the unimodal dark type characteristic of the early part of the year.

A feature of particular interest is the apparent disappearance of the pale mode during the last month of the dry season; this observation lends support to the view, based on pupal searches (Glasgow, 1953), that at this time the eluvial breeding ground is completely evacuated, larviposition being confined to the evergreen vegetation of the drainage lines. The significance of this evacuation becomes clear when we consider that in the previous month the pale mode reached the pigmentation index level of 5. Reference to fig. 2a shows that this level is indicative of a relative humidity of about 20 per cent.*; and it has already been shown that a 40 per cent. mortality may be expected at this humidity (Bursell, 1958). It must further be remembered that since emergence occurs in the late afternoon (see, for instance, Bursell, 1959) and since there is a 1- to 2-hour flightless period after emergence, the flies have little chance of obtaining a blood-meal until the day after emergence, so the water reserves have to suffice for about 16 hours' post-emergence existence. Thus conditions in the eluvial breeding grounds are clearly inimical to survival at this time of the year, and in the absence of alternative breeding grounds the population would be subject to very heavy mortality. The results suggest that in areas of this type, characterised by prolonged and severe dry seasons, clearing of riverine thicket would hold out some promise of success as a control measure, through an effect on pupal water balance.

* No allowance need be made for differences in size, see above.

Direct measurement of soil humidity.

Some attempt was made to check the above findings by direct measurement of soil-space humidities using a Gregory Humidity Meter (Negretti and Zambra). The element could be inserted to various depths in the soil by means of a specially constructed metal probe, made so that free diffusion of air to the element could take place only from the soil layers at element level. A period of 24 hours was allowed for equilibration before readings were commenced. Unfortunately some unseasonal showers of rain fell in early October so that the records made in November may not strictly represent conditions at the end of the dry season. It was found that in a typical eluvial breeding site of *G. pallidipes* (a small thicket of *Combretum parvifolium*) the relative humidity at a depth of 12 cm. was 85 per cent. and at a depth of 4 cm. 50 per cent., the mean ambient humidity at this time being 30 per cent. There was no indication of diurnal variation in the readings taken at 4 and 12 cm. depth, such variations being presumably damped by the resistance to diffusion offered by the surface layers of the soil.

Unfortunately the heavy rains broke before observations could be extended to cover sites in the riverine thicket; all that can be said, then, is that direct measurements of soil-space humidities support the concept of a humidity gradient extending through the upper layers of the soil as put forward in an earlier publication (Bursell, 1958) and implicit in the demonstration of a seasonal variation of pigmentation. Such measurements, furthermore, are not at variance with the view that at the height of the dry season humidities near the surface of the soil in typical breeding sites may reach very low values, close, in fact, to those of the ambient atmosphere.

The burrowing of larvae.

The existence of a gradient of humidity through the upper layers of the soil suggests that, during the dry season, larvae might avoid exposure to critical levels of humidity during subsequent stages of development by burrowing more deeply. Dr. Burtl has in fact noted that puparia of *G. pallidipes* recovered in the early months of the dry season were found within about 1-3 cm. of the surface, while at the height of the dry season most of the puparia were buried to a depth of 5-8 cm. (personal communication). Some attempt was made to study the effect of humidity and temperature on the burrowing of larvae in order to provide an experimental basis for these observations.

A cubical wooden framework, 10 × 10 × 10 cm., was constructed, five of the sides of the cube being covered with single sheets of filter paper. Into this container, soil from pupal sites was poured after prior equilibration in shallow trays exposed to the desired humidity. The soil boxes were placed in glass jars of suitable dimensions in such a way that the soil surface was within 3 cm. of a perspex lid. The latter was furnished with three apertures of about 2.5 cm. diameter into which could be fitted the standard maintenance tubes covered at the lower end with coarse-mesh mosquito gauze. Females of *G. pallidipes* near the end of pregnancy were confined in the maintenance tubes and the newly deposited larvae made their way through the mosquito netting to drop on to the surface of the soil. The temperature inside the glass jars was controlled by means of a thermoregulator with an electric bulb as a source of heat, and humidity was controlled by solutions of potassium hydroxide or by calcium chloride contained at the bottom of the jars. After 25-30 larvae had been deposited, the soil boxes were taken out and successive 1-cm. layers of soil removed, a record being made of the number of puparia found in each layer.

There is some tendency for the top layers of the soil to be deficient in puparia under conditions of low relative humidity, while the deeper layers tend to carry

an excess as compared with the distribution in 90 per cent. R.H. (fig. 4a). However, when the distributions were tested on the null hypothesis no significant difference could be established with the numbers available ($\chi^2 = 1.72$, with 3 degrees of freedom). The distribution of pupae at 21 and 31°C. is shown in

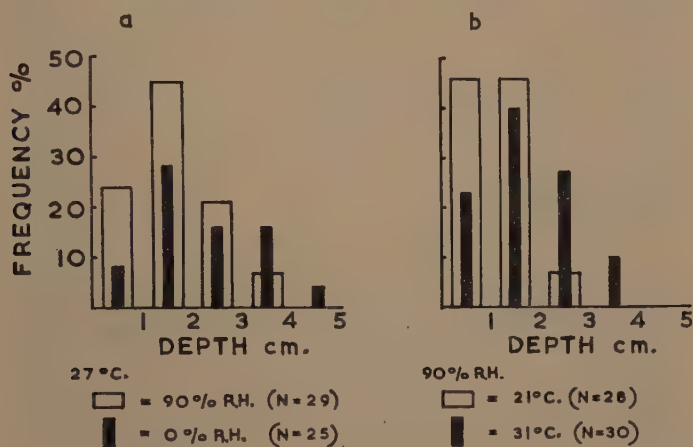


Fig. 4.—The effect of humidity (a) and temperature (b) on the depth to which larvae of *G. pallidipes* burrow.

fig. 4b, relative humidity being 90 per cent. in both cases. There appears to be a tendency for larvae to burrow more deeply at high temperatures, but again the distributions do not differ significantly. However, if the results obtained at 27 and 31°C. are combined, a significant difference can be established between these higher temperatures and 21°C. ($\chi^2 = 10.24$ for 3 d. of f.; $P = 0.01-0.02$).

It seems, then, that the greater depth to which larvae burrow at the end of the hot season can be considered mainly as a response to high temperature; there is a possibility that the effect may be enhanced by the low humidities characteristic of this season.

Other species.

The possible effect of humidity on coloration was tested on four other species of tsetse fly, namely *G. swynnertoni* Aust., *G. morsitans* Westw., *G. palpalis fuscipes* Newst. and *G. longipennis* Corti. There was some indication of a slight effect on the pigment spot of the second abdominal segment in *G. swynnertoni* but the pigmentation of the abdominal bands was unaffected. In none of the other species could an effect of humidity on the extent of abdominal coloration be demonstrated. For *G. morsitans* this lack of effect accords with the observation that there is no seasonal variation of colour (Dr. E. Burt, personal communication); but the apparent absence of an effect on *G. palpalis* was surprising in view of the differences in pigmentation reported by de Barros Machado (1954) for this species, differences which could be correlated with the density of vegetation in the habitat. The number of examples of *G. palpalis* studied during the present work was small, and the subject would be worth a more thorough investigation using different subspecies.

Summary.

The extent of pigmentation of the abdominal bands of *Glossina pallidipes* Aust. was studied in specimens emerging in the laboratory from puparia

maintained at constant temperature and a range of relative humidities and derived from females collected in the field at Shinyanga, Tanganyika. An index of pigmentation was obtained by regarding the bands as consisting in all of 15 zones, each carrying a score of 1.

The index was closely dependent on the humidity experienced during pupal development, almost full pigmentation being produced in saturated air and almost complete suppression of it in dry air; it is inversely related to size and little affected in nearly saturated air by temperatures below 28°C. during pupal development, although still higher temperatures reduce it quite sharply.

In flies collected in the field throughout the year, most of those taken towards the end of the rains (March and April) fell into the darker pigment categories; as the dry season advanced the distribution tended to become bimodal, with the darker mode relatively steady at an index of about 12 and the paler mode moving progressively down the scale, reaching an index of about 5 in October and then disappearing. December and January collections (rainy season) were again unimodal, resembling those of March. It is suggested that these changes reflect the use of two types of larviposition site, the darker mode representing pupae from the evergreen thickets along the drainage lines and the lighter mode those from semi-deciduous thickets on the eluvial slopes, and that during the dry season the soil-space humidity in the latter sites may reach levels inimical to survival.

The depth to which larvae of *G. pallidipes* burrow appears to be related to the temperature, and perhaps the humidity, obtaining at the time of larviposition.

The possible effect of humidity on coloration was tested in four other species of tsetse fly, namely *G. swynnertoni* Aust., *G. morsitans* Westw., *G. palpalis fuscipes* Newst. and *G. longipennis* Corti. Only *G. swynnertoni* gave indications of some slight effect.

Acknowledgements.

My sincere thanks are due to Dr. E. Burt for most helpful discussion of the problems involved and for permission to quote unpublished work on the breeding of *G. pallidipes*. Also to Mr. Yahya Mohamed for his care in the maintenance of breeding populations and for the preparation of mounted specimens of samples taken during my periodic absences from Shinyanga; and to Mr. C. J. Webb for the photographic material.

References.

- DE BARROS MACHADO, A. (1954). Révision systématique des Glossines du groupe *palpalis* (Diptera).—*Publ. cult. Cia Diamant. Angola* no. 22, 189 pp.
- BURSELL, E. (1958). The water balance of tsetse pupae.—*Philos. Trans. (B)* **241** pp. 179–210.
- BURSELL, E. (1959). The water balance of tsetse flies.—*Trans. R. ent. Soc. Lond.* **111** pp. 205–235.
- GLASGOW, J. P. (1953). Tsetse research.—*Rep. E. Afr. Tsetse Tryp. Res. Reclam. Org.* 1952 pp. 10–21.
- JACKSON, C. H. N. [1954]. Tsetse research.—*Rep. E. Afr. Tsetse Tryp. Res. Reclam. Org.* 1953 pp. 20–28.
- VICARS-HARRIS, N. H. (1936). *Glossina swynnertoni*, Austen, in relation to various vegetation types.—*Bull. ent. Res.* **27** pp. 533–557.



The abdominal banding of females of *G. pallidipes* derived from puparia maintained at different relative humidities: a, at 98 per cent.; b, at 40 per cent.; c, at 20 per cent.

FURTHER OBSERVATIONS ON LAKE-SIDE AND RIVERINE
COMMUNITIES OF *GLOSSINA PALPALIS FUSCIPES*
NEWSTEAD.

By E. BURSELL and J. P. GLASGOW

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From earlier work on *Glossina palpalis fuscipes* Newst., it had been concluded that riverine communities of this species were permanently in a state of greater hunger than lake-side communities (Glasgow, 1954). This conclusion was based on analysis of catches (percentage of teneral flies† in the whole catch, and percentage of females among non-teneral flies) and on a behaviour criterion (percentage of non-teneral males caught on the party, the remainder being taken from the ground and from vegetation). It seemed desirable to test the validity of these criteria of hunger by direct estimation of the fat content of samples from the two types of habitat, and simultaneous collections were accordingly made, in Nyanza Province, Kenya, from the Kabwoch forest area of the upper Kuja

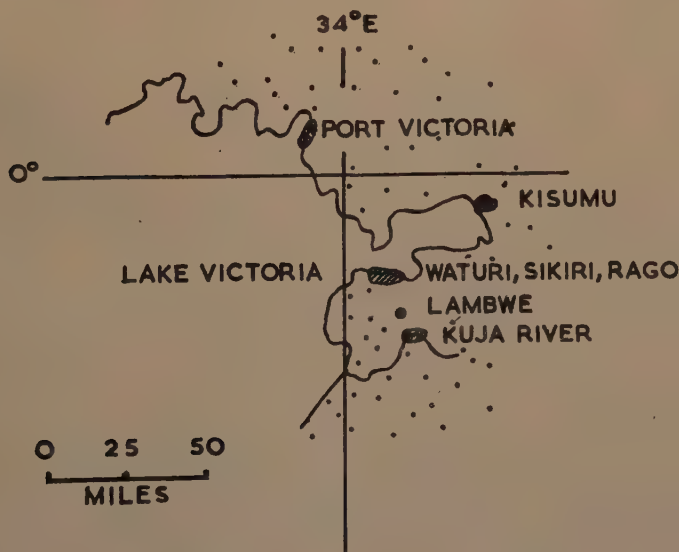


Fig. 1.—Map showing the areas in Nyanza Province, Kenya, sampled and discussed.

river, a riverine site near that used in the earlier work, and from the lake shore at Waturi and Rago, two adjacent peninsulas in the Kavirondo Gulf, Lake Victoria, 25 miles distant from the Kuja river and some 50 miles from Port Victoria, where the original lake-side observations had been made (see map, fig. 1). The size of flies was also determined, on the grounds that differences in the state

* This paper comes from the Entomological Research Laboratory, Shinyanga, Tanganyika.

† Teneral tsetse flies are those which have not yet taken their first blood-meal.

of nutrition of the two populations might be reflected in corresponding size differences.

The length of the middle part of the fourth longitudinal vein was used as a measure of size, and the loss of weight in chloroform as a measure of fat, both procedures being carried out as in Buxton (1955, pp. 709-710). Contrary to expectation, it was found (Table I) that the lake-side flies were slightly but

TABLE I.

The size and fat content of males of *G. palpalis fuscipes* from lake-side and riverine habitats.

			Kuja river	N	Waturi-Rago	N
(a) Vein length (mm.)						
1955	October	..	1.444 ± .005	79	1.426 ± .004	101
1956	January	..	1.468 ± .006	50	1.449 ± .004	120
	April	..	1.458 ± .005	80	1.445 ± .004	109
	May	..	1.439 ± .007	50	1.432 ± .004	151
(b) Fat content (mg.)						
1955	October	..	1.55	83	2.10	102
1956	January	..	1.58	52	1.47	126
	April	..	2.07	96	1.96	113
	May	..	1.78	51	1.58	171

Fat content was determined on bulked samples so that no estimate of error is available.

significantly *smaller* than the river flies on three occasions, the size difference becoming insignificant in May, towards the end of the wet season. The fat content was variable, and it was clear that the expectation of more fat in the lake-side flies was not fulfilled.

An attempt was therefore made to investigate the matter further; the results obtained, although by no means conclusive, were thought of sufficient interest to warrant publication in their present state, since it is unlikely that we shall have an opportunity to confirm or extend them.

Material and methods.

Simultaneous collections were made from Waturi and from the Kabwoch forest area of the upper Kuja river. Waturi is the peninsula which was the scene of the defoliation experiment in 1952 described by Fryer, Johns & Yeo (1957). The vegetation was apparently back to normal by 1955. Mr. J. M. B. Harley informs us (personal communication) that in February 1952, before the application of the defoliant, he took 81.3 per cent. of non-teneral males on the party, out of a sample of 705. This is as high as any observed by us (Table IV) and indicates that the results recorded in Table IV are not related to any lingering disturbance of the vegetation. The Kabwoch forest is some distance upstream from the areas investigated by Glasgow (1954). Samples of flies were taken by three African assistants on paths cut as near as possible to the edge of the water, and puparia were obtained from sites adjacent to the collection paths but usually further removed from the water's edge. Non-teneral flies for comparison were collected about two weeks after the puparial samples were taken; with the temperatures obtaining at this time of the year such flies would have emerged from puparia deposited somewhat earlier than those samples; but since there was no differential

variation in the size of puparia taken from the two sites during the period in question, the lack of more accurate timing will not affect the conclusions drawn.

The size of puparia and the size and fat content of flies were determined according to methods described elsewhere (Bursell, 1958, 1960). Non-teneral flies were dried before being sent to Shinyanga, so that for comparison with measurements made on fresh teneral flies a correction had to be made for the slight shrinkage that occurs during desiccation (2.2% of the desiccated size); the measure of size is linear, being in fact the area of the thorax in arbitrary units.

Results.

A summary of results obtained with male flies is given in Table II. Since there appeared to be no difference between the sexes in respect of the characteristics under consideration the corresponding figures for females have been omitted. A few data from Sikiri, a larger peninsula east of Waturi, are also shown in Table II.

TABLE II.

The size of puparia (both sexes) and the size and fat content of males of *G. palpalis fuscipes* from riverine and lake-side habitats.

	Kuja river	N	Waturi	N	Sikiri	N
(a) Puparia						
Surface area (mm. ²)						
Collected 24.i.58	49.74 ± .29	19	45.86 ± .37	19		
" 11.ii.58	48.37 ± .36	19	45.20 ± .28	19		
" 11.iii.58	48.69 ± .31	20	45.05 ± .30	20	43.11 ± .58	6
(b) Teneral flies*						
(i) Thoracic surface	7.57 ± .085	15	6.807 ± .052	15		
(ii) RDW (mg.)	4.907 ± .070		4.644 ± .067			
(iii) Fat content (mg.) (at RDW 4.908)	1.655 ± .073		1.642 ± .55			
(iv) b (mg. fat/mg.RDW) ..	+0.6653		+0.6562			
(c) Non-teneral flies						
(i) Thoracic surface						
Collected 5.ii.58	7.576 ± .136	15	7.277 ± .070	15		
" 26.iii.58	7.420 ± .073	20	7.154 ± .073	20	6.730 ± .116	20
(ii) Fat content (mg.)						
Collected 5.ii.58	1.70 ± .10		1.43 ± .15			
" 26.iii.58	2.73 ± .15		1.93 ± .11		1.51 ± .11	

RDW = residual dry weight (*i.e.* dry weight minus fat)

b = regression coefficient

The thoracic surface is measured in arbitrary units. The fat content of non-teneral flies was determined with batches of 10 flies, and variation between batches forms the basis for the estimates of error.

* Determinations made on flies freshly emerged from the puparia collected on 24.i.58.

Three collections of puparia were made at Waturi and the Kuja river (Table IIa); measurements showed that there was a slight decrease in size during the course of observations, but that the changes were commensurate in the two areas of investigation. In all samples the puparia from the Kuja river were significantly larger than those from Waturi, and the single sample from Sikiri had the smallest mean size of all.

Emergence of flies from these puparia was rather poor, and only the first collection provided sufficient numbers to enable an estimate to be made of teneral size and fat content. The samples from Kuja and Waturi showed a difference in size of the same magnitude as that characteristic of puparia (about 8%) but there was no significant difference in fat content once allowance was made for the difference in size (see Table IIb).

The non-teneral flies from the Kuja river were found to be slightly larger than the Waturi ones (Table IIc), in accord with previous wing-vein measurements. But the difference amounted to less than 4 per cent. compared with the difference of over 8 per cent. recorded for puparia and teneral flies. The reason for this discrepancy is made clear by consideration of the frequency distributions of sizes shown in fig. 2. At Kuja there is no difference between the teneral and the

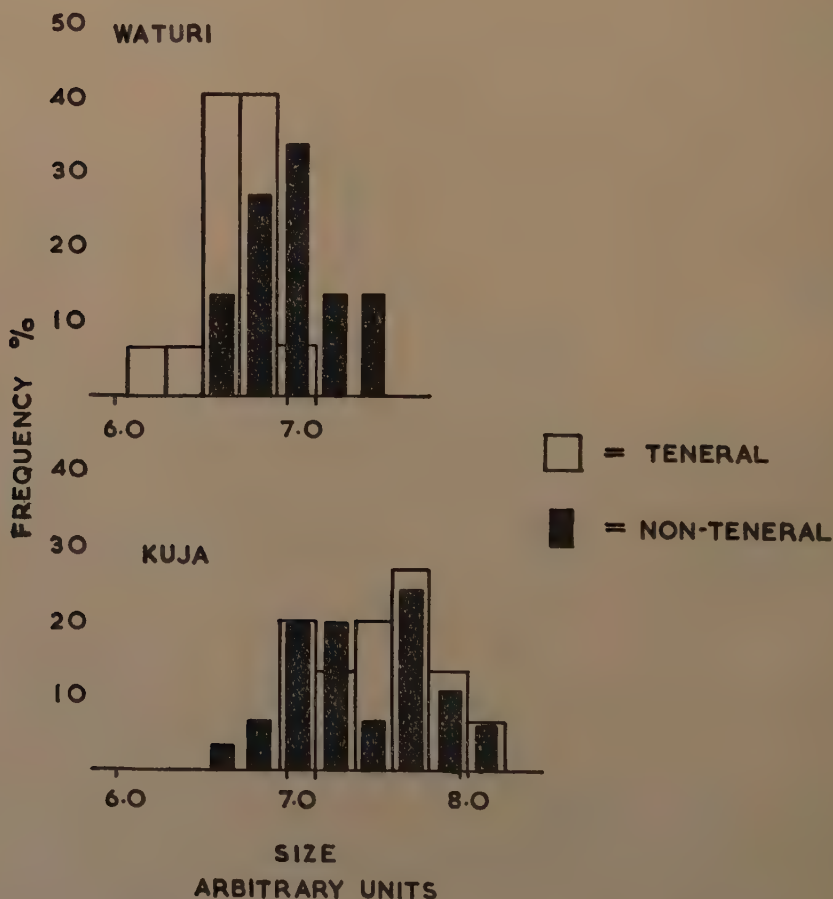


Fig. 2.—The frequency distributions of size for teneral and non-teneral examples of *G. palpalis fuscipes* at Waturi and the Kuja river.

non-teneral distributions, but at Waturi comparatively few of the smaller size classes are represented in the non-teneral sample. There appears, in other words, to have been a selection for size at Waturi with consequent reduction in the observed size difference between non-teneral samples.

It is, of course, possible that this apparent selection for size represents an artefact resulting from a bias in sampling. But it is difficult to see how a sample of adult flies of size greater than average, or a sample of puparia of size smaller than average, should have been collected at Waturi and not at Kuja, since the sampling technique was the same in the two places, and it seems justifiable to ignore this possibility.

Jackson (1948) reported a similar selection for size in *G. swynnertoni* Aust. during the early dry season, the observed shift in the frequency distribution being such as could be accounted for by a 10 per cent. mortality of flies below average size. Inspection of the distributions in fig. 2 suggests that the comparable mortality factor for *G. palpalis* would be very much greater, but in view of the small samples under consideration it has not been thought worth while to make a numerical estimate. Jackson (1944) also recorded for *G. morsitans* Westw. what may be another instance of differential elimination of teneral flies. In his fig. 4, it is shown that teneral females become much more numerous relative to teneral males in the hot dry season. Since females are bigger than males, this effect could be produced by greater mortality of the smaller, male, flies.

Since the relation between the size of puparia and the size of flies which emerge from them is known to be very nearly linear over parts of the size range as small as those recorded in Table IIa (Bursell, The effect of temperature on the consumption of fat during pupal development in *Glossina* ‡), an estimate of the size of teneral flies may be made from the size of puparia obtained at the second collection for comparison with the second collection of non-tenerals. These estimates, together with the actual figures of the first collection, already discussed, are set out in Table III. It is clear that both at Waturi and at Sikiri there is a

TABLE III.

The difference in size between teneral and non-teneral males of *G. palpalis fuscipes* from riverine and lake-side habitats.

Place	Date collected	Thoracic surface		Difference
		Teneral	Non-teneral	
Waturi	5.ii.58	6.81	7.28	0.47
	26.iii.58	6.64	7.15	0.51
Sikiri	26.iii.58	6.24	6.73	0.49
Kuja river	5.ii.58	7.57	7.58	0.01
	26.iii.58	7.37	7.42	0.05

The thoracic surface of teneral flies at 26.iii.58 has been estimated from the size of the puparia collected two weeks previously.

very marked difference in size between teneral and non-teneral flies, reflecting a heavy elimination of the lower size-groups, while at the Kuja river the difference is negligible.

From the relations between fat, size and teneral dry weight it can be calculated that the fat content at emergence of those flies that survive long enough to feed is 1.71 mg. while that of flies that fail to do so is 1.17 mg. Given the lethal lower limit of fat content and the relation between size and fat consumption at the temperature obtaining during the present investigation (Bursell, 1959) it can be calculated that these fat stores would suffice to maintain life at rest for 102

‡ To appear in a later part of *Bull. ent. Res.*

and 90 hours, respectively. It seems reasonable to suppose that this difference in potential survival period is sufficient to eliminate the smaller flies. The possibility that their elimination may have been due to desiccation is very unlikely; for one thing, the relation between water content and size, unlike that between fat content and size, is such that the water reserves are proportionately the same over the complete range of sizes, so that small flies are at no disadvantage in this respect; secondly, conditions in the habitat of *G. palpalis* near the lake shore are fairly humid, and this species is no more susceptible to desiccation than most others (Bursell, 1959).

The possibility that smaller flies are eliminated after the first blood-meal rather than before it is also unlikely, for the fat content of non-teneral flies appears to be largely independent of size, being a function rather of the past history of the individual (Bursell, unpublished).

The fat content of flies captured at Waturi, Sikiri and on the Kuja river are shown in Table IIc. For the February samples there was no significant difference, but in March the lake-side flies had much less fat than the riverine flies, and the difference was far greater than could be accounted for by the slight difference in size (see regression coefficient and size difference in Table IIb). In general, the results confirm the impression gained from the comparisons discussed above, namely that the lake-side communities are 'under stress' as compared with the riverine ones.

Fly-round data were regrettably not available from Waturi at the time the flies considered in Table II were collected, nor from Kuja on either occasion. The only data we have are from the lake shore at Rago and Waturi during 1955-56, when the flies analysed in Table I were collected. They are presented in Table IV.

TABLE IV.

Analysis of catch and behaviour of *G. palpalis fuscipes* on two lake-side fly-rounds.

	Rago				Waturi			
	Teneral (%)	N.T. ♀♀ (%)	N.T. ♂♂ on party (%)	A.D.	Teneral (%)	N.T. ♀♀ (%)	N.T. ♂♂ on party (%)	A.D.
1952 Feb.	—	—	—	—	—	—	81	(6)
1955 Aug.	9	6	1	828 (2)	8	6	1	977 (4)
Sept.	19	8	23	969 (3)	14	7	10	742 (11)
Oct.	12	5	38	855 (3)	15	7	34	741 (4)
Nov.	11	8	59	647 (5)	11	15	62	503 (4)
Dec.	6	14	71	457 (8)	7	15	68	506 (8)
1956 Jan.	6	6	71	277 (8)	5	5	57	443 (8)
Feb.	8	7	68	428 (5)	6	7	61	591 (5)
Mar.	14	14	90	519 (4)	9	14	81	655 (5)
Apr.	7	12	84	336 (3)	8	8	82	676 (2)

Teneral (%)

= Percentage of all flies which are teneral.

N.T. ♀♀ (%)

= Percentage of non-teneral flies which are female.

N.T. ♂♂ on party (%)

= Percentage of non-teneral males caught from party, the balance coming from the ground or vegetation.

A.D.

= Apparent density, catch of non-teneral males per 10,000 yards traversed. Numbers in brackets indicate how many times each round was done.

In August, September and October the catch composition was similar to that previously described as typical for lake-side communities at Port Victoria (Glasgow, 1954). But in subsequent months the percentage of males caught on the party rose to levels normally only encountered with riverine communities. During the same period there was a fall in apparent densities, caused to some extent, perhaps, by the high teneral death-rates discussed above. These changes coincided with the gradual onset of the hot dry season, a circumstance which makes one suspect that the differences between the lake-side communities at Port Victoria and at the Kavirondo Gulf peninsulas might be referable to a difference in climate.

Some comparison of climate between these places is made possible by the existence of meteorological records from the Lambwe Valley (see map, fig. 1) which overlap with early work at Port Victoria and with some records made at Sikiri in 1954 (Johns, 1957). All records were made in Stevenson screens, and the lake-side records are closely comparable in so far as both meteorological stations were set up in a thicket zone just inland from the true habitat of *G. palpalis*. Using the average of the sum of mean monthly maximum and mean monthly minimum temperatures in February and March as an index it is found (see fig. 3) that in 1950 the Port Victoria temperatures were about 0.5°C. lower

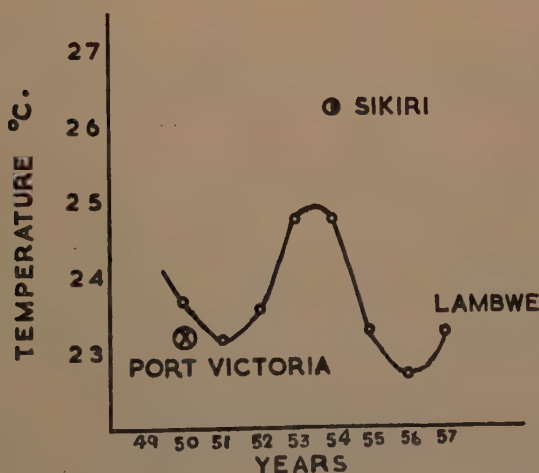


Fig. 3.—The average of mean monthly maximum and mean monthly minimum temperatures during February and March at Lambwe, Port Victoria and Sikiri.

than the Lambwe ones, while in 1954 the Sikiri values were about 1.5°C. higher; in other words, temperatures in the Kavirondo Gulf at this time of the year seem to be about 2°C. higher than those obtaining along the northern shores of Lake Victoria, the saturation deficits being correspondingly greater.

It seems not unreasonable to suggest that climatic differences of this kind might be directly responsible for the stresses which appear to be acting on communities of the Kavirondo Gulf as compared with Port Victoria and the Kuja river. More particularly, the situation at Waturi could be taken to reflect a general nutritional deficiency associated with rapid utilisation of food reserves as determined by the higher temperatures. Thus, given similar conditions as

regards the frequency of host encounter, a high rate of utilisation of food reserves would be expected to increase the proportion of hungry flies in the population, and this would be reflected in an increase in the percentage of males caught on the party and in a decreased fat content; a similar effect on the nutrition of the pregnant female would lead to the production of smaller puparia (Buxton & Lewis, 1934; Mellanby, 1937); and in the teneral population, a high rate of fat consumption would lead to a heavy selection for size.

Effects of this kind but operating in favour of the lake-side communities, might well explain how a distinction came to be drawn between these and riverine communities, for the high and evenly distributed rainfall that generally characterises the lake shore as compared with the hinterland would be associated with a lowering of temperatures and hence with less hungry populations of tsetse. Whether the recorded differences can in all cases be ascribed to simple climatic differences of this kind cannot be determined in the absence of more extensive meteorological data from the regions concerned, but the present comparison between the Kuja river and Waturi constitutes a clear exception to the original rule.

Discussion.

Catch composition and behaviour records are two of the most widely used criteria by which the physiological state of a population of *Glossina* is judged (see Buxton, 1955). The present results (Tables I and II) show a progressive decrease in the size of flies and puparia during the hot dry season (January–March), which suggests that at this time the population is short of food; and since the period is characterised by a high proportion of non-teneral males caught on the party, it would seem that this behavioural criterion may have a real meaning in terms of nutritional status; it also appears to be a very responsive indicator, taking values between 1 and 90 per cent. in the course of the year. The proportions of tenerals and of female non-tenerals, on the other hand, appear to be completely valueless as criteria of physiological state under the conditions of the present investigation. They remain at a level close to that characteristic of previously described lake-side communities in spite of the heavy stresses acting during the hot season at Waturi—stresses reflected in the high percentage of males caught on the party, the high teneral death-rate, the low fat content, the low apparent densities and the production of small puparia. It would seem that changes in female and teneral percentages recorded in the literature and in Table IV may not in fact be simply related to changes in nutritional state of the population as has hitherto been generally supposed. Differences between places at one time may well have a different significance from variations between occasions at one place, and a reassessment of the significance of such changes seems to be needed.

Summary.

Earlier work in Nyanza Province, Kenya, had led to the conclusion that riverine communities of *Glossina palpalis fuscipes* Newst. were permanently hungrier than lake-side communities. This was based on analysis of catches (percentage of teneral flies in the whole catch, and percentage of females among non-teneral flies) and on a behaviour criterion (percentage of non-teneral males caught on the party), but subsequent observations in the two types of habitat, in which a different area was used to represent the lake side, showed the lake-side flies to be slightly smaller than the riverine flies and not to differ in fat content, and a further investigation was accordingly made.

Puparia were collected on three dates between January and March 1958 and their surface area measured. A measure of the thoracic surface and fat content

was taken of all adults emerging. Non-teneral flies were collected, for comparison, about two weeks later than the puparia.

In all samples, the riverine puparia were significantly larger than those from the lake side, and flies that emerged showed a comparable difference in size, but not in fat content corrected for size. Non-teneral riverine flies were slightly larger than lake-side ones but the difference was less than half that shown by the puparia and the teneral flies obtained from them. Evidence is adduced to show that this discrepancy is due to elimination of the lower size-groups in the lake-side community. Estimates of fat content of non-teneral flies support the conclusion that the lake-side community was under stress as compared with the riverine one, and analysis of available fly-round data from the lake side also suggests stress conditions.

The lake-side results are at variance with those from the site used in the earlier work. Available meteorological data show that the average temperature during February and March is 2°C. higher at the present site than at the former; such difference may directly cause the stresses that appear to be operating in the present instance.

The results suggest that the percentage of non-teneral males caught on the party has a real meaning in terms of nutritional status, and that it is also a very responsive indicator, but that the proportions of tenerals and of female non-tenerals may not be simply related to the nutritional state as had hitherto been supposed.

Acknowledgements.

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References.

- BURSELL, E. (1958). The water balance of tsetse pupae.—*Philos. Trans. (B)* **241** pp. 179–210.
- BURSELL, E. (1959). The water balance of tsetse flies.—*Trans. R. ent. Soc. Lond.* **111** pp. 205–235.
- BURSELL, E. (1960). The measurement of size in tsetse flies (*Glossina*).—*Bull. ent. Res.* **51** pp. 33–37.
- BUXTON, P. A. (1955). The natural history of tsetse flies.—*Mem. Lond. Sch. Hyg. trop. Med.* no. 10, 816 pp. London, Lewis.
- BUXTON, P. A. & LEWIS, D. J. (1934). Climate and tsetse flies: laboratory studies upon *Glossina submorsitans* and *tachinoides*.—*Philos. Trans. (B)* **224** pp. 175–240.
- FRYER, J. D., JOHNS, D. L. & YEO, D. (1957). The effects of a chemical defoliant on an isolated tsetse fly community and its vegetation.—*Bull. ent. Res.* **48** pp. 359–373.
- GLASGOW, J. P. (1954). *Glossina palpalis fuscipes* Newst. in lake-side and in riverine forest.—*Bull. ent. Res.* **45** pp. 563–574.
- JACKSON, C. H. N. (1944). The analysis of a tsetse-fly population. II.—*Ann. Eugen.* **12** pp. 176–205.
- JACKSON, C. H. N. (1948). Some further isolated generations of tsetse flies.—*Bull. ent. Res.* **39** pp. 441–451.

- JOHNS, D. L. (1957). A study of the population dynamics and ecology of *Glossina pallidipes* Austen.—Thesis, Bristol Univ.
- MELLANBY, H. (1937). Experimental work on reproduction in the tsetse fly, *Glossina palpalis*.—*Parasitology* **29** pp. 131–141.

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THE AVAILABILITY OF THE COCONUT BUG, *PSEUDOTHERAPTUS WAYI* BROWN, (COREIDAE).

By F. L. VANDERPLANK

E.M.N

Yeo & Foster (1958) describe a technique for counting the numbers of *Pseudotheraptus wayi* Brown, on coconut palms, and claim that the total nymphal populations, and the proportions of them in the various stages, are sufficiently consistent to suggest that this searching technique may give reproducible results, whereas Vanderplank (1958) is of the opinion that the results of searching for nymphs are too variable and inconsistent to be of value unless very large numbers of palms are climbed, the cost of which would be prohibitive.

Searches for adults and nymphs have been carried out under my supervision for six years in Zanzibar, and during this time nearly a quarter of a million palms have been searched and the results recorded. The two senior climbers were also used by myself on Mafia Island in 1955 and their services loaned to the Colonial Pesticides Research Unit. A comparison of their catches in Mafia with those in Zanzibar suggests that the behaviour of *P. wayi* varies between the two islands, but a more important fact is that the analysis of the data shows that the availability of nymphs of *P. wayi* varies with the time of day and the weather conditions.

Observations.

At least 200 palms were searched daily, six days a week, for two years in one particular area in Zanzibar. Ten climbers were employed, and their individual catches did not differ significantly, but the total day-to-day catch of nymphs of *P. wayi* varied from 0 to 72, even though the searches were arranged to cover a cross-section of the area. Such a large daily variation would not occur fortuitously even were the insect's distribution* to be, as claimed by Yeo & Foster (1958), not at random.

The days on which climbers failed to catch any nymphs of *P. wayi* were bright and sunny, and it appeared that there was a correlation between light intensity

TABLE I.

The effects of weather conditions on the catch of nymphs of *P. wayi*.

Weather conditions	No. nymphs caught (A)	No. palms searched (B)	No. palms searched per nymph caught (B/A)
Bright sunny days	52	2,340	45
Quarter to half sky with clouds ..	128	1,865	14.5
Cloudy but not overcast	79	680	8.5
Overcast	41	640	15.5

* The distribution of *P. wayi* is affected by that of the red tree ant, *Oecophylla* sp., and undoubtedly by the presence of certain species of lizards. In areas where *Oecophylla* does not occur, *P. wayi* is found in all the palms except those, about one per cent., that are inhabited by these lizards. The dominant species of ants was recorded for each of the numbered palms, which were searched at three-monthly intervals.

and the availability of *P. wayi*; however, on very dull days the numbers caught fell. This might indicate that there was an optimal light intensity when *P. wayi* fed in the open, or that on very dull days the nymphs became more difficult for the searchers to see.

The results obtained from analysis of the catches from the 100-acre control (unsprayed) plot at Kizimbani during 1957 are given in Table I. The palms were climbed between the hours of 9.0 a.m. and 11.0 a.m. local time, each day. The same climbers were used throughout these observations, which were spread over six months, and various types of weather conditions were interspersed at random, so the differences in numbers of palms searched per nymph caught are not due to any seasonal changes in nymphal populations. These figures suggest an inverse relationship between sunlight and availability, and prompted an attempt to make more accurate and detailed observations.

TABLE II.

Availability of adults and nymphs of *P. wayi* at different periods during bright, sunny days and clear nights.

Period (East African local time)	Number of searches	No. of searches in which nymphs were observed		No. of searches in which adults were observed	
		%		%	
2.0—4.0 a.m.	4	4	100	3	75
4.0—6.0 a.m.	18	15	83	10	56
6.0—8.0 a.m.	28	6	21	4	14
8.0—10.0 a.m.	54	6	11	2	4
10.0 a.m.—noon	43	3	7	0	0
noon—2.0 p.m.	25	4	16	0	0
2.0—4.0 p.m.	30	23	77	7	23
4.0—6.0 p.m.	47	47	100	36	76
6.0—8.0 p.m.	35	35	100	29	83
8.0—10.0 p.m.	20	20	100	16	80
10.0 p.m.—midnight	10	10	100	8	80

No searches were made between midnight and 2.0 a.m.

Two young palms in Livingstone House garden commenced fruiting early in 1958 and were immediately infested by *P. wayi*. Since these palms were only ten feet high they offered an excellent opportunity to observe both nymphs and adults of *P. wayi* at all times of the day and night and in all weather conditions. The number of searches, each of which occupied less than 20 minutes, made in each successive 2-hour period during the day, and the proportion of them in which nymphs, or adults, were found, are given in Tables II and III. The observations recorded in Table II were carried out when the sky was less than one-quarter covered by clouds. From 4.0 p.m. to 4.0 a.m., nymphs were seen in every search and adults in the great majority of them, whereas from 10.0 a.m. to 2.0 p.m. no adults were observed and nymphs only occasionally. During these hours of bright sunlight the nymphs could be found, with difficulty, hiding in crevices at the base of the coconut spadix or in the debris that collects in the axils of the leaves. On two occasions adults were found hiding in this debris. Only nymphs and adults that could be observed without probing the crevices or searching the debris are considered in Tables II and III. The observations carried out in the same palms, between the hours of 4.0 a.m. and 8.0 p.m., on

dull days, which occurred fortuitously during the same period as those in Table II, are summarised in Table III. At least half the sky was covered by cloud in each of these observations.

TABLE III.

Availability of adults and nymphs of *P. wayi* at different periods during cloudy days.

Period (East African local time)	Number of searches	No. of searches in which nymphs were observed		No. of searches in which adults were observed	
		%		%	
4.0—6.0 a.m. 	21	21	100	15	71
6.0—8.0 a.m. 	55	55	100	45	82
8.0—10.0 a.m. 	43	41	95	33	77
10.0 a.m.—noon 	43	38	88	29	67
noon—2.0 p.m. 	38	29	76	19	50
2.0—4.0 p.m. 	25	14	56	9	36
4.0—6.0 p.m. 	40	32	80	30	75
6.0—8.0 p.m. 	22	19	86	16	73

When the two Tables are compared and the difference examined by the χ^2 test it is found that, for each of the 2-hour periods between 6.0 a.m. and 2.0 p.m. (in the case of nymphs) or 4.0 p.m. (in the case of adults), the proportion of searches in which *P. wayi* was observed is significantly greater on dull days than on bright days. There is no significant difference between dull and bright days in respect of the observed presence of *P. wayi* during any other 2-hour period for which comparisons can be made, except 4.0 to 6.0 p.m., when the proportion of searches disclosing nymphs was greater on bright days. A few observations carried out on cloudy nights showed that adults and nymphs of *P. wayi* could be observed on each occasion.

Observations have also been made on the behaviour of nymphs and adults of *P. wayi* in light, medium and heavy rain. In a very slight drizzle or slight rain with small raindrops, neither adults nor nymphs appear to be affected and remain exposed in the open; but when the intensity or size of the raindrops increases, both adults and nymphs move to the underside of the *vidaka*, or nutlets. In very heavy rain they may have to retreat further into some crevice. There seems to be no shortage of niches or crevices that remain dry even during the heaviest of downpours, when on some occasions rain has been falling at the rate of two inches an hour.

Discussion.

Yeo & Foster (1958) claim that "the total nymphal populations, and the proportions of them in various stages are sufficiently consistent to suggest that the searching technique may give reproducible results and thus be of considerable value as a means of assessing the results of control measures". Their observations were carried out over a very short period and a relatively small number of palms was searched. The observations recorded above suggest that the time of day and the amount of cloud (or light intensity) may cause significant differences in the numbers of nymphs or adults seen or caught and must be taken into account if this method is used to assess the result of an application of insecticide.

Summary.

Reasons for the large day-to-day variations in the numbers of nymphs and adults of the Coreid bug, *Pseudotheraptus wayi* Brown, taken in the crowns of coconut palms in Zanzibar by the searching technique over a period of six years were investigated in 1957-58. Data are given showing the results of searches (each occupying less than 20 minutes) carried out on two young palms at different times of day and night and in different weather conditions. For each successive 2-hour period between 6.0 a.m. and 2.0 p.m. (in the case of nymphs) or 4.0 p.m. (in the case of adults) the proportion of searches in which *P. wayi* was observed was significantly greater on dull days than on bright, sunny days, but there were no such differences that were significant in respect of any other 2-hour period for which comparisons could be made, except 4.0 to 6.0 p.m., when the proportion of searches disclosing nymphs was greater on bright days. During the hours of bright sunlight, the adults and nymphs hide in crevices and in the debris found in the leaf axils, but both remain in the open from dusk to dawn. During heavy rain they take shelter in dry crevices and niches.

It is pointed out that this behaviour must be taken into consideration if the searching technique is used to assess the result of an application of insecticide.

References.

- VANDERPLANK, F. L. (1958). Studies on the coconut pest, *Pseudotheraptus wayi* Brown (Coreidae), in Zanzibar. I. A method of assessing the damage caused by the insect.—*Bull. ent. Res.* **49** pp. 559-584.
- YEO, D. & FOSTER, R. (1958). Preliminary note on a method for the direct estimation of populations of *Pseudotheraptus wayi* Brown on coconut palms.—*Bull. ent. Res.* **49** pp. 585-590.

THE EFFECTS OF DIFFERENT PLANT FOODS ON THE FECUNDITY,
FERTILITY AND DEVELOPMENT OF A COTTON STAINER,
DYSDERCUS SUPERSTITIOSUS (F.).

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In an earlier publication, Geering (1953) reported the successful breeding of *Dysdercus supersticiosus* (F.) on young sorghum (*Sorghum vulgare*) grains both in the field and laboratory.

In the present work, after it had been demonstrated that *D. supersticiosus* could breed (i.e., that adults laid fertile eggs and the nymphs from these developed successfully to adults which likewise laid fertile eggs) when fed only on young sorghum grains, a more careful study was made of the suitability of sorghum as a host-plant. This was done by comparing the fecundity (numbers of eggs per female), fertility (percentage hatching of eggs) and development of nymphs, on the two diets; (A) young sorghum grains, and (B) a normal food, viz., ripe seed of Upland cotton (*Gossypium hirsutum*). The young sorghum grains were supplied when in the milky stage, fully grown but with the endosperm not yet fully converted to starch. In the field, this stage was reached 16 days after bursting of the stamens.

In addition, an examination was made of the comparative suitability of contrasting types of sorghum; other plants outside the Malvales were also tested and some were found suitable. In continuation of the work by Pearson (1934) and Rainey (1948), breeding on cotton bolls of different ages was also studied. Experiments with a diet of cotton seed from which the oil had been extracted, or that had been subjected to heat, were also included.

The results from these experiments are presented here and are briefly discussed in relationship to the nutritional factors required for the breeding of plant-feeding insects.

The method employed for the rearing of stainers used in these experiments has already been described by Geering (1956).

Comparison of fecundity and fertility of adults of *D. supersticiosus* maintained on (A) young sorghum grains and (B) ripe cotton seed.

Throughout these experiments, the standard cotton and sorghum diets have been, respectively, seeds of the cotton variety BP52, soaked in water for 24 hours, and milky grains of a semi-dwarf, close panicked, medium maturing variety of sorghum (code no. J.53, from the Agricultural Experiment Station at Serere, Uganda), similar in habit to a variety which was observed to be severely attacked by *D. supersticiosus* in the field in Nigeria.

In the first experiment the insects used originated from a series of six generations bred in captivity on cotton seed. One hundred nymphs were reared to maturity on each of the two diets, and 20 pairs of adults withdrawn and maintained on the same diet. The number of eggs, viable eggs and egg batches produced per female in the two groups are shown in Table I. Use has been made

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of a logarithmic transformation to obtain values of M_w (Haddow, 1960, p. 779) for each of these variables.

Examination of these figures shows that in all the factors except fertility the two groups differed markedly, cotton seed being consistently more suitable for breeding than the young sorghum grains. This comparison, however, is based

TABLE I.

Fertility, fecundity and length of life of adult females of *D. supersticiosus* (in 20 pairs) reared and maintained on seeds of (A) sorghum and (B) cotton.

	Number of eggs per ♀ (fecundity)		Number of viable eggs per ♀		% viability (fertility)		Number of batches per ♀		Length of life (days)	
	A	B	A	B	A	B	A	B	A	B
Mean log ($x+1$)	1.69	2.19	1.12	1.82	1.34	1.63	0.33	0.56	1.21	1.36
S.E.	0.17	0.17	0.18	0.18	0.16	0.10	0.04	0.05	0.05	0.04
P	<0.05		<0.01		N.S.		<0.01		<0.02	
M_w	47.98	153.88	12.18	65.07	20.88	41.66	1.14	2.63	15.21	21.90

x represents the actual counts for individual females.

on adults that were reared as nymphs on the different diets, and their resultant fecundity may have been as much affected by the diet during nymphal development as during adult life.

The comparison was repeated, therefore, but with the use of adults that had been collected as fifth-instar nymphs on ripe cotton in the field and allowed to develop to maturity in the laboratory on cotton seed. When mature, the adults were divided at random between the two diets. Owing to a severe bacterial disease amongst the colonies at that time, however, only 14 pairs became available for observation in each treatment. The results are shown in Table II.

TABLE II.

Adults of *D. supersticiosus* (14 pairs) reared on cotton and then transferred to seeds of (A) sorghum and (B) cotton.

	Number of eggs per ♀		Number of viable eggs per ♀		% viability (fertility)		Number of batches per ♀	
	A	B	A	B	A	B	A	B
Mean log ($x+1$)	1.95	1.85	1.73	1.64	1.74	1.65	0.50	0.47
S.E.	0.23	0.25	0.22	0.26	0.09	0.15	0.07	0.08
P	N.S.		N.S.		N.S.		N.S.	
M_w	88.13	69.79	52.70	42.65	53.95	43.67	2.16	1.95

No statistically significant differences occur between the groups fed on the two diets, and on the basis of the two experiments shown in Tables I and II it would appear that the food of the developing nymphs may have an overriding effect on their fecundity when adult. Thus, young sorghum grains were as good as cotton seed in promoting fecundity when the nymphs had been reared on cotton seed; but when the nymphs were reared and maintained on sorghum, fecundity was reduced to approximately one third of that on cotton seed. The fertility of eggs appeared to be unaffected by the two diets. The adults survived for a shorter time when reared on sorghum, and the reduced fecundity was associated more with fewer batches than with smaller numbers of eggs per batch.

The investigations were continued in order to assess the fecundity and fertility of females derived from nymphs reared on one diet and transferred to the other when newly moulted to adult. The four comparisons were:

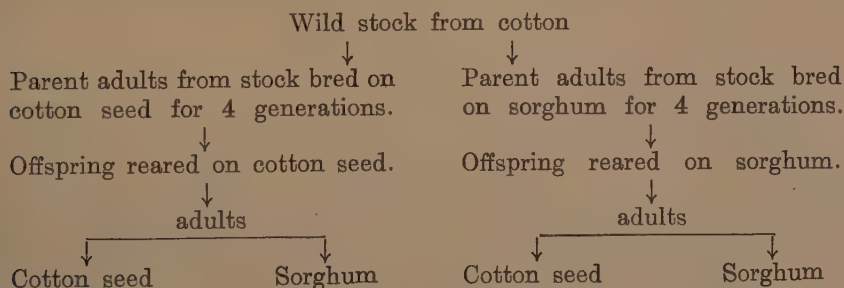
(A) Reared and left on sorghum.

(B) Reared and left on cotton seed.

(A-B) Reared on sorghum and transferred to cotton seed.

(B-A) Reared on cotton seed and transferred to sorghum.

The origins of the different groups are shown schematically below.



The results, presented in Table III, indicate a much lower level of fertility than in the first two tests, possibly attributable to the effect of a disease which was at the time killing and deforming a high proportion of the adults, and of which a concurrent symptom appeared to be lowered fertility. However, eight pairs that had moulted to the adult stage on the same day were set up for each treatment.

TABLE III.

Effect of an alteration of diet, at time of final ecdysis, on fecundity and fertility of *D. supersticiosus* (8 pairs).

	Number of eggs per ♀				Number of viable eggs per ♀			
	A	B-A	B	A-B	A	B-A	B	A-B
Mean log ($x + 1$) ..	1.85	1.89	2.19	2.53	1.03	0.39	1.08	1.92
S.E.	0.41	0.28	0.34	0.06	0.32	0.27	0.41	0.07
P	N.S.				<0.01			
M _w	69.79	76.62	153.88	337.84	9.72	23.55	11.02	82.18

For explanation of symbols, see text.

In this experiment, those nymphs reared on cotton and transferred to sorghum laid half as many eggs than those reared and kept on cotton—in marked contrast to the previous experiment—while those reared on sorghum and transferred to cotton laid twice as many as those kept on cotton, but these differences were not significant, whereas differences in viability were significant.

It would thus appear that in this experiment the diet of the developing nymph had less effect on subsequent fecundity than in the earlier experiments, and fecundity seemed to be largely determined by the adult diet. The reason for this is not immediately apparent. The results in Table III are, however, in agreement with those shown in Table I in that nymphs reared and kept on sorghum laid fewer eggs than those reared and kept on cotton, and this may be due in part to a size difference in the adults reared on the two diets.

An examination of the size of individuals reared on the two diets was therefore made. The measurements made were the maximum width of the pronotum, and maximum length of the hemielytron. These multiplied together give a measure of the dorsal area of the insect; it is not known to what extent this is correlated with gross weight.

Males and females were measured separately. The results given in Table IV show that both males and females reared on cotton seed were larger than those reared on sorghum.

TABLE IV.

Frequency distribution of dorsal area of adults of *D. supersticiosus* reared on (A) sorghum and (B) cotton.

Area (sq. mm.)	Males				Females			
	A		B		A		B	
	No.	%	No.	%	No.	%	No.	%
41-45	4	3.7	2	1.7	0	0.8	0	0
46-50	19	17.6	9	7.5	1	0.8	0	0
51-55	18	16.7	16	13.3	1	1.6	0	0
56-60	23	21.3	25	20.8	2	11.0	1	0.8
61-65	32	29.6	46	38.3	14	15.1	3	2.5
66-70	10	9.3	20	16.7	19	15.9	15	4.1
71-75	2	1.8	2	1.7	20	19.8	16	13.2
76-80	0	0	0	0	25	17.5	27	22.3
81-85	0	0	0	0	22	15.9	26	21.5
86-90	0	0	0	0	20	1.6	37	30.6
91-95	0	0	0	0	2	0	5	4.1
96-100	0	0	0	0	0	0	1	0.8
Total individuals	108		120		126		131	

Nymphal development on cotton and sorghum.

The effects of the different diets were further examined by following the rates of development, and mortalities, of the nymphs when reared on cotton seed or young sorghum grains. Quantities of food supplied were in excess of one day's requirements and were changed each day.

The results are summarised in Table V.

The total nymphal development period and the mortality were greater on sorghum than on cotton, and, in other comparisons of colonies reared on the two diets, mortality percentages ranged from 9 to 33 in the case of cotton, and 26 to

73 in that of sorghum. Mortality occurred predominantly during the second instar, thus confirming earlier observations made in the development of the mass-rearing system (Geering, 1956).

It may thus be concluded that although *D. supersticiosus* is able to reproduce and develop when fed on young sorghum grains, these are less suitable than ripe cotton seeds.

TABLE V.

Mortality and developmental period of nymphs of *D. supersticiosus* on cotton and sorghum.

Instars	Sorghum					Cotton				
	II	III	IV	V	II-V	II	III	IV	V	II-V
No. started ..	50	19	11	11	50	50	29	25	24	50
Died	31	8	0	1	40	21	4	1	1	27
Range in days	7-16	7-16	10-14	15-19	45-55	7-16	7-11	9-14	15-20	40-54
Av. days ..	11.2	9.5	11.9	15.8	49.9	8.7	8.2	10.4	16.8	44.3

Fecundity of *D. supersticiosus* on different varieties of sorghum.

Circumstantial evidence suggesting that some varieties of sorghum may be more suitable than others for the breeding of *D. supersticiosus* was reported from Nigeria (Geering, 1953). The position observed there was that an indigenous dwarf variety, 'Kaura', was heavily infested in the field and, as a result of extensive breeding of the bug, severely damaged, whilst nearby crops of the other major indigenous variety 'Fara fara', a tall, open-panicled type, were not infested. Further observations by Baillie (1953) confirmed this behaviour of *D. supersticiosus* in the field, when these two varieties were grown in adjacent plots.

Accordingly, seeds of the two varieties were obtained from Nigeria, and grown in Uganda at the Cotton Research Station. Two similarly contrasting types from Serere Experiment Station were also grown, and the behaviour of *D. supersticiosus* on these was compared, in the laboratory, with those on a standard diet of cotton seed. The adults placed on the different foods originated from a parental stock reared on cotton seed. Characteristics of the different food-plants are given below:

Food-plant	Code no. or name	Origin	Description
A 1 Sorghum	Fara fara	Nigeria	Tall, open-panicled, white grain
A 2 "	Kaura	"	Dwarf, close panicled, yellow grain
A 3 "	Kabi	Uganda	Tall open-panicled, yellow grain
A 4 "	J. 53	"	Semi-dwarf, close panicled, brown grain
B Cotton	BP52	"	Commercial variety

'Kabi' has a longer maturation period than the other three varieties, namely 113 days as compared with 70-90 days, from germination to flowering. The age of the grains supplied as food was the same for all varieties, viz., 16 days from

flowering; the state of physiological development of these grains may, however, have differed between the varieties.

The quantities of food supplied per pair of stainers were, in the case of the sorghum, 40 grains per two days, and with cotton, 6 seeds per day. Water was also supplied. Ten pairs were placed on each diet, and the total eggs and viable eggs for each pair on the different diets are shown in Table VI.

TABLE VI.

Fecundity and fertility of adults of *D. supersticiosus* (10 pairs) fed on (A) different sorghums and (B) on cotton seed

	Number of eggs per ♀					Number of viable eggs per ♀				
	A1	A2	A3	A4	B	A1	A2	A3	A4	B
Mean log ($x + 1$)	1.94	1.44	1.83	1.57	2.35	1.35	1.24	1.50	1.16	1.84
S.E.	0.23	0.25	0.21	0.27	0.04	0.29	0.22	0.18	0.26	0.11
P	<0.05					N.S.				
M _w	86.1	26.5	66.5	36.2	229.9	21.4	16.4	30.6	13.5	68.2

The results reveal an unexpected situation in the light of the field observations in that the Fara fara variety (A 1) proved more suitable for egg-production than Kaura (A 2). This suggests that there may be some factor in the field that causes *D. supersticiosus* to select Kaura in preference to Fara fara. The same relationship held good for the similar contrasting types from Uganda; but there has been no record obtained in the field there of *D. supersticiosus* breeding on any variety of sorghum.

Fecundity on seeds of other crops.

It has also been observed in Nigeria that *D. supersticiosus* can breed on bulrush millet (*Pennisetum typhoides*) in the field (Geering, 1953).

In order to confirm this, adult stainers that had been reared on cotton were fed on young milky grains of *Pennisetum* and the egg-production was recorded. At the same time, young cobs of maize (*Zea mays*) from which the sheaths had

TABLE VII.

Fecundity and fertility of adults of *D. supersticiosus* (10 pairs), fed on seed of (A) sorghum, (B) cotton and (C) maize.

	Number of eggs per ♀			Number of viable eggs per ♀		
	A	B	C	A	B	C
Mean log ($x + 1$)	1.75	2.37	2.03	1.25	2.04	1.45
S.E.	0.30	0.10	0.08	0.30	0.08	0.18
P	N.S.			N.S.		
M _w	55.23	233.42	106.15	16.78	108.65	27.18

been stripped were similarly tested and the suitability of these was compared with the standard sorghum and cotton diets. The results are shown in Table VII, but the bulrush millet diet had to be stopped before the stainers had completed their full oviposition cycle, owing to failure of supplies of grains, and the results obtained with it are thus not included in the table.

The only figures obtained for bulrush millet were for the first batches of eggs. These totalled 343 eggs from seven females, and were much smaller than the first batch on any of the other three diets.

The result of feeding with maize is interesting; it was provided in the form of young cobs from which the sheaths had been removed. It was found later that the adults would, if confined on complete cobs, feed through the sheaths, pair and lay eggs. It is at an earlier stage in the life-cycle that the sheaths prevent breeding, for second-instar nymphs are unable to penetrate the sheaths and reach the young grains, and all die. When second-instar nymphs were provided with stripped cobs, 33 per cent. matured to the adult stage compared with 42 per cent. on cotton.

The results described above show that a range of grain crops may contain, in varying amounts, the requisite factor or factors necessary for successful reproduction of *D. supersticiosus*. What then is the position with regard to other plant orders? Rainey (1948) has already commented on this aspect: "The absence of breeding on food plants outside the Malvales, such as *Acacia pallens* Rolf. (Leguminosae) and *Gymnosporia acuminata* Szysz. (Celastraceae) (Pearson, 1937) may also be interpreted as evidence of specific protein requirements for oviposition, similar, for example, to those of many blood-sucking insects." This opinion was based on laboratory breeding and on field observations, which showed that adults of *Dysdercus* fed, but did not breed, on the plants mentioned. The successful breeding of *D. supersticiosus* on grain crops in the laboratory, therefore, seemed to justify examining the Leguminosae, for example; Rainey's conclusions were based on experiments and observations on *D. nigrofasciatus* Stål.

Two species of legume were accordingly examined: the garden dwarf bean (*Phaseolus* sp.) and the cowpea (*Vigna unguiculata*). On young pods of *Phaseolus*, 4 inches in length, (i.e., 6 days from flowering) nymphs were unable to develop, and adults laid no eggs. On young cowpea pods of the same size, nymphs developed but suffered a high mortality. Adults reared to maturity on cotton seed, and then transferred to cowpea, laid slightly less than one-sixth of the number of eggs laid by related adults reared and left on cotton seed. These results are shown in Table VIII.

TABLE VIII.

Fecundity and fertility of *D. supersticiosus* (10 pairs) reared on cotton seed and (B) left on cotton seed or (D) transferred to young pods of cowpea.

	Number of eggs per ♀		Number of viable eggs per ♀	
	B	D	B	D
Mean log ($x + 1$)	1.55	0.79	1.63	0.79
S.E. 	0.34	0.28	0.32	0.24
<i>P</i>	N.S.		N.S.	
<i>M_w</i>	34.48	5.17	41.66	5.17

It can be seen that, in the case of *D. supersticiosus*, the leguminous diets provided did not wholly prevent egg-production although a marked degree of inhibition was evident. If a specific protein requirement is necessary (Rainey, 1948), then it may well diminish in quantity progressively in the seeds of the Malvales, Gramineae and Leguminosae.

Fecundity of *D. supersticiosus* fed on cotton bolls of different ages.

Rainey (1948) gave figures showing changes in composition of the developing boll, and demonstrated that from the second week onwards the percentage of crude protein steadily increases, reaching a maximum in the ripe seed. The oil content also shows a similar increase with age. Some information had been previously obtained by Pearson (1934, 1937) on the suitability of bolls of different ages for the nymphal development of *D. nigrofasciatus*, and Rainey, commenting on this, stated that "The progressively better growth obtained in older bolls, and the need for access to split fruit, may perhaps be associated with the low protein content of the younger bolls." The same two authors have shown that males of *D. nigrofasciatus* feed preferably on young bolls, which have a higher sugar content, while fifth-instar nymphs and adult females feed mainly on bolls aged 2-5 weeks old, which provide a diet equally rich in sugars and proteins, the reducing sugars decreasing with increasing age of the boll. No information appears to be available on the age of boll most suitable for egg-production, but it was, however, frequently observed in Nigeria (Geering, 1953) and in Northern

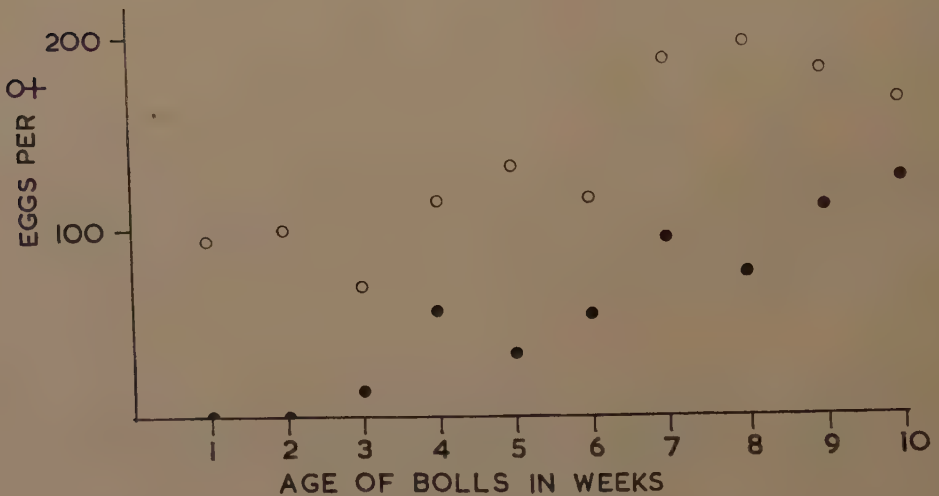


Fig. 1.—Total number of eggs laid by females of *D. supersticiosus*, when fed on cotton bolls of different ages, during 12 and 24 days after commencement of diet.
●, eggs per female at 12 days.
○, eggs per female at 24 days.

Rhodesia (Bebbington & Allan, 1936) that although adults of *D. supersticiosus* entered cotton fields early in the flowering of the crop, no second-instar nymphs appeared until the first bolls were splitting, suggesting that older bolls were necessary for successful oviposition.

Accordingly, at Namulonge, cotton flowers were labelled as they opened throughout the season, and, after 10 weeks, ten groups of related adults of *D. supersticiosus* (reared on cotton seed) were set up on bolls of different ages, from one to nine weeks old, and on ginned cotton seed stored from the previous season. A week later, another group was placed on 10-week-old bolls. In order to facilitate recording, adults on bolls of each age were kept in one large cage, and provided with a common supply of food. Five pairs of adults were placed on bolls of 1-4 weeks old, and ten pairs on bolls of each of the remaining ages. Eggs were collected daily from these colonies of *Dysdercus*, counted and incubated in order to test fertility.

The result for each colony, after 12 and 24 days from commencement of each diet of bolls and expressed as the average number of eggs per female, is shown in fig. 1. After 12 days, groups on 1- and 2-week-old bolls had laid no eggs. A comparison of the minimum preoviposition periods is presented in fig. 2, the longest preoviposition period resulting from a diet of the youngest bolls, decreasing as the age of the bolls increased. The older bolls, and the one-year-old cotton seed, gave the minimum preoviposition period.

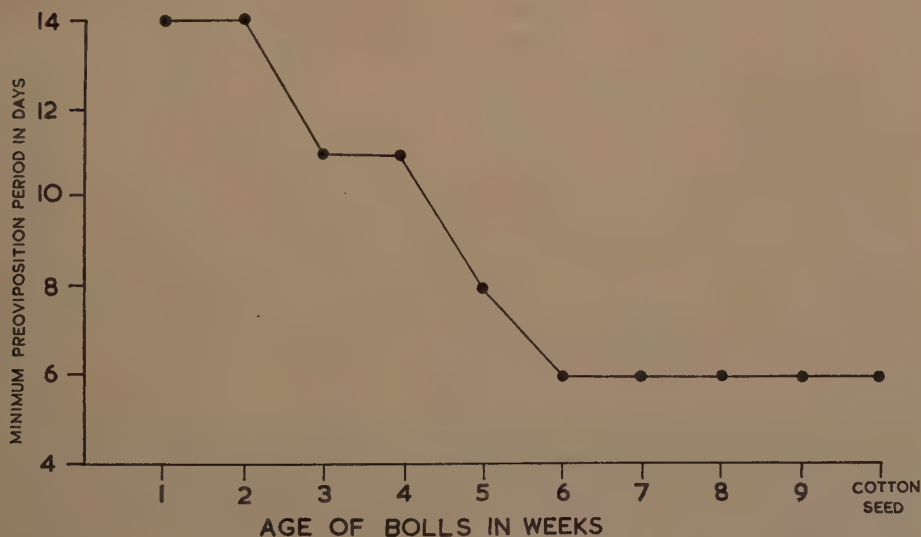


Fig. 2.—Graph showing minimum preoviposition period, in days, of females of *D. supersticiosus* when fed on cotton bolls of different ages and on stored cotton seed.

The experiment was repeated in the following year, employing exactly the same technique, the only difference being that an adequate supply of bolls of all ages was assured. This enabled the experiment to be continued for a much longer period and to allow ten pairs of stainers on bolls of each age group. The total eggs laid after 24 days showed a similar but more consistent relationship with age of the bolls than was the case in the previous experiment (Table IX). The experiment was continued until either all females were dead, or until no eggs had been laid by the survivors for two weeks. In the results presented, the oviposition period is calculated as the period between the dates of laying of the first and last batches of eggs.

TABLE IX.

Fecundity of 10 females of *D. supersticiosus* fed on cotton bolls of different ages and on stored cotton seed.

Age of bolls (weeks)	Eggs per female after 24 days	Total eggs per female	Oviposition period in days	Rate of egg- production (eggs per female per day)	Surviving females
1	22	63	55	1.1	5
2	56	111	48	2.3	7
3	64	104	48	2.2	5
4	56	64	17	3.7	6
5	46	72	33	2.2	0
6	102	105	26	4.0	0
7	76	95	30	3.2	1
8	134	171	32	5.3	1
9	161	175	27	6.5	1
10	109	129	31	4.1	0
Cotton seed	71	78	19	4.1	4

It is apparent that stainers feeding on bolls of different ages show differences in rate of egg-production (fig. 3), these being more closely related to age of the bolls than are the differences in total egg-production. There was a longer survival of females on the youngest bolls. In this experiment, the maximum

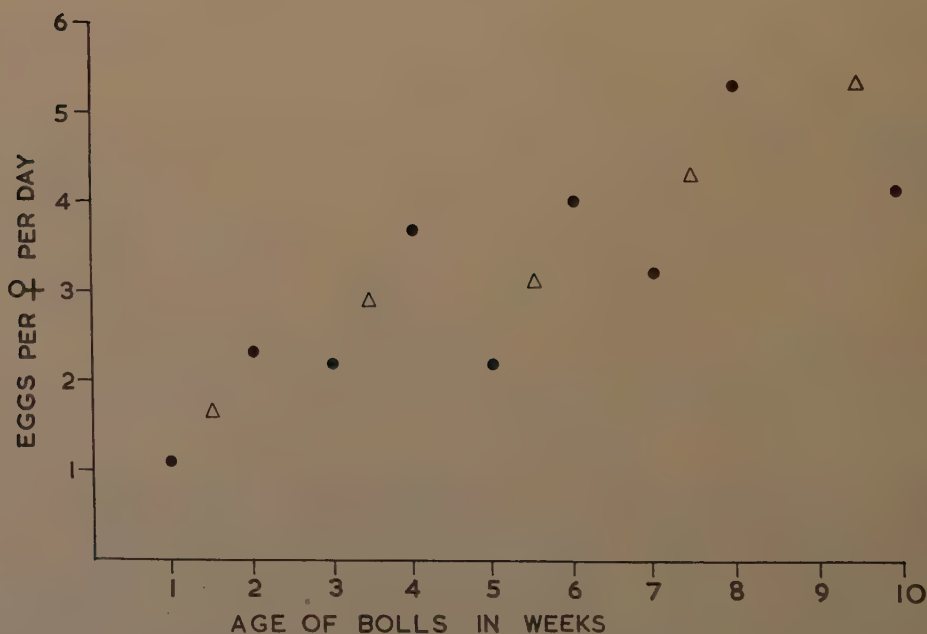


Fig. 3.—Mean number of eggs laid per day by females of *D. supersticiosus* when fed on cotton bolls of different ages.

△, means of successive pairs of age groups of bolls.

egg-production was not on cotton seed, which suggests that changes involving the factors essential for egg-production might occur in the seed during prolonged storage.

Adult fecundity and fertility and nymphal survival of *D. supersticiosus* when fed on treated cotton seed.

(a) Seed from which the oil had been extracted.

Two batches, each of ten pairs of adults, were fed on cotton seed from which the oil had been extracted with petroleum ether for 24 hours in a soxhlet apparatus. The cotton seed fed to one of the batches had previously been soaked overnight, in water, and that fed to the other batch had no water added. In the latter treatment no adults survived longer than eight days and no eggs were laid. With water present, the mean number of eggs laid per female and the fertility (Table Xa) were less than from those fed on untreated seed (Table Xb, control), indicating that removal of oil from the cotton seed has some effect on the fecundity. Nymphs that hatched from those eggs were fed on similarly treated seed and survived with no marked effect on the duration of each stadium, although a mortality rate of 85 per cent. was recorded in the first instar, which is higher than that normally experienced when the adults are fed on normal cotton seed. The results do, however, indicate that cotton-seed oil is not entirely necessary for either survival or breeding of stainers.

(b) Heat-treated seed.

Cotton seed was heated in an oven at varying temperatures for one hour and then fed to adult stainers, with and without added water. When water was not available, no eggs were laid, as in the previous experiment. In the other treatment, with added water, the mean number of eggs laid by ten females decreased significantly with the higher temperature treatments (Table Xb) so that the number of eggs laid by adult females fed on seed treated at 190°C. was less than 10 per cent. of that in the control treatment. Viability was likewise affected. Lengths of adult survival periods and number of batches of eggs laid were not altered by the various treatments. Second-instar nymphs suffered a greatly increased mortality when fed on seed heated at the highest temperature, but the duration of stadia was not altered. This inability of the second-instar nymphs to survive on cotton seed heated to high temperature may have been partly due to a change in the physical nature of the seed or seed coat. There is a suggestion that those that survived experienced lower mortalities in the succeeding instars. In another experiment, adults of *D. supersticiosus* fed on seed that had been heat treated for two hours, exhibited a similar reduction in fecundity and fertility with the higher temperatures, *e.g.*, 100, 150 and 190°C. The nymphs, however, were only able to survive on the seed heated at 50 and 100°C., with a high mortality in the younger instars. In the remaining two treatments, *i.e.*, 150 and 190°C., none of the nymphs reached the adult stage although some did survive up to the third and fourth instars.

Discussion.

In all the experiments, the effect of diets has mainly been measured by fecundity of the females and viability of the eggs. Where individual pairs were used, males were replaced, as they died, by others reared on appropriate diets. When larger groups were fed on separate diets, *i.e.*, cotton bolls of different ages, male mortality was not always greater than female mortality and hence replacement of males was not always necessary.

It is possible, therefore, that the apparent effect of diets on female fecundity is the result of a combined effect on both males and females. It may, however,

TABLE X.

(a) Fecundity and fertility of adults and survival and development of nymphs of *D. supersticiosus* when fed on cotton seed from which the oil had been extracted.

	No. eggs laid per ♀	No. of viable eggs per ♀	Mean % viability
Mean of 10 adult females	264.2	75.0	30.7
S.E. ±	173	62	23

Nymphal survival and development

Instar	No.	Period (days)	No. died	% mortality
I	750	—	638	85.0
II	112	7	30	26.7
III	82	12	13	15.8
IV	69	13	5	7.2
V	64	13	5	7.8

(b) Fecundity and fertility of adults of *D. supersticiosus* (10 pairs per treatment) and instar length and mortality of nymphs fed on cotton seed treated for 1 hour at various temperatures (with water added).

Treatments (°C.)	No. eggs laid per ♀	No. viable eggs per female	Mean % viability	Adult length of life
Control ..	433.1	185.0	42.7	49
30	467.0	241.9	51.8	49
50	356.0	163.2	45.8	45
70	262.3	106.6	40.6	45
100	249.9	162.4	64.9	30
130	294.6	195.8	66.4	31
150	191.5	95.0	49.6	44
170	51.4	16.4	31.9	44
190	41.3	10.7	25.9	62

Instar length (days) and mortality of nymphs (% mortality in parentheses)

°C.	Instar length (days)			
	II	III	IV	V
30	9	10	10	19
50	10 (25.4)	7 (12.4)	10 (12.4)	23 (12.4)
70	10	15	14	19
100	9 (25.5)	11 (5)	9 (4.6)	20 (4.4)
130	8	10	12	25
150	12	15	18	21
170	13	13	13	23
190	10 (95.5)	10 (8.9)	10 (4.5)	20 (4.5)
Control \ ..	10	10	13	20

be significant that variations in fecundity are very much greater than variations in fertility, *i.e.*, in the percentage of eggs hatching.

Before considering these results, which have a bearing on several aspects of insect nutrition, and seeking some interpretation of them, it is worth while to review briefly results of similar experiments obtained by other workers. Both Trager (1947) and Friend (1958), discussing the nutrition of phytophagous insects, have pointed out that little is known about their essential food requirements, that some evidence is available to show that different foods can have distinct effects on the reproductive capacity of certain insects, and that, likewise, the food obtained as a larva may have a profound effect on the adult in this respect. With regard to food selection, Trager concluded: "... this appears to be determined in most cases by characters of the foods which have no direct connection with fundamental nutritional requirements . . .". The results obtained with *D. supersticiosus* on sorghum agree with these statements and conclusions.

Dahms, Snelling & Fenton (1936) showed that the chinch bug, *Blissus leucopterus* (Say), also exhibited different fecundities on different varieties of sorghum; but in this instance the adults were feeding on the vegetative parts of the young plants. Creighton (1938) discussing "Factors influencing insect abundance," with reference to *Dysdercus suturellus* (H.-S.) concluded, on the basis of laboratory feeding experiments, that "... the food of adult *Heteroptera* will tend to affect their reproductive capacity, and thereby their abundance." Wigglesworth (1950, p. 477) refers to experiments by Trouvelot & Grison (1935) with *Leptinotarsa*, where it was shown that fecundity varies with the variety of potato on which the larvae are reared, and that fecundity also declines on foliage of increasing age. Raw (1951) describes two experiments with the garden chafer, *Phyllopertha horticola* (L.); where adults were either fed on a mixed diet or given no food, there was no evidence that feeding significantly affected fecundity, but it increased the rate of egg-production: in the second experiment, adults were fed on burnet (*Poterium sanguisorba*) and laid significantly more eggs than those on other diets such as bracken, blackberry or grass. He concludes that "It is difficult to reconcile the results of these two experiments, and need for further investigation of the effect of feeding on oviposition is evident." All the conclusions reached by these workers are applicable to the data presented here.*

Lethicin is apparently the chemical factor involved in the case of *Leptinotarsa*, but there is no direct evidence of what substance or substances there may be in the developing cotton boll that could influence the reproduction of *Dysdercus*. Rainey's boll analyses showed progressive increases in total nitrogen from the second week, and a steady rise in oil content. On the evidence then available, he suggested that a specific protein might be required for successful breeding, admittedly with a different species (*D. nigrofasciatus*), and that this protein only occurred in the Malvaes; it may be, however, that this is also a fat-soluble factor common to the Malvaes which increases in the developing bolls, but this is difficult to define since seed from which the oil had been extracted did not wholly impair the egg-production of females of *D. supersticiosus*.

The question now arises as to what are the factors which permit successful egg-production and nymphal development? Are they the same in seeds other than those of the Malvaes and are the different suitabilities of the various food-plants for satisfactory breeding of *Dysdercus* related to differing contents of these same factors? The results obtained from the experiment in which bolls of different ages were fed to the adult stainers may possibly indicate that factors

* Later work on *P. horticola* has shown that, in this species, the average female does not begin feeding until the major part of her eggs is laid (Milne, 1959), a very different behaviour from that of *Dysdercus*, and one that accounts for earlier conclusions that, in *P. horticola*, adult feeding affects neither the number of eggs produced in the ovaries, nor the number laid (Milne & Laughlin, 1956).

necessary for oviposition increase in quantity as the age of the boll increases. A change in concentration of these factors would produce the observed differences in rate of egg-production. It is known that cotton-seed oil contains 40–55 per cent. of linoleic acid (Hilditch, 1947) and a high concentration of vitamin E (Harris, Quaife & Swanson, 1950), both of which substances have been shown by Fraenkel & Blewett (1946) to be necessary factors for normal growth and emergence of three species of *Ephestia*. It is possible, therefore, that an increased quantity of one or both of these substances in the developing cotton boll could account for the progressive increase in rate of egg-production by adults noted here, and for the better development of nymphs noted by Pearson (1934, 1937) on older bolls. However, this hypothesis is not supported by the results obtained from feeding adults on seed from which the oil has been extracted, from which both the linoleic acid and vitamin E would have been removed; but since the nymphal stages of the adults observed were not fed on a similar diet, but on normal cotton seeds, the utilisation of these products may have occurred during this early period of development, with an ultimate effect upon adult egg-production. The increase in crude protein with increase in age of the boll, indicated by Rainey's results, may possibly be another factor associated with the higher rate of egg-production which is obtained after feeding with older cotton bolls. The diminution in egg-production shown by adult females fed on seed heated at 150 to 190°C. may have been due to the destruction of the protein together with other accessory food factors.

With this preliminary information gained, it should now be possible to begin a more extensive study of the nutritional factors required by *Dysdercus* for successful breeding. Two difficulties in technique, which are regarded as giving a possible explanation for some of the discrepancies noted, are:

(a) The consistent standardisation of the different natural diets. The physiological age of young milky sorghum grains will have varied greatly; and it is not known to what extent breeding is affected by this. There are also indications that the age of the cotton seed, *i.e.*, time in store since harvesting, may influence the breeding of stainers feeding on this diet.

(b) Maintaining, under laboratory conditions, a stock of healthy stainers with high fecundity and fertility; a problem that has been reported by several workers in the past.

Summary.

Dysdercus supersticiosus (F.) is capable of utilising a much wider range of food-plants than was previously supposed, and is able to complete a full breeding cycle on the several diets other than cotton. This has been demonstrated by rearing and breeding adults and nymphs in the laboratory, in Uganda, on selected food material, *e.g.*, *Sorghum vulgare*, *Pennisetum typhoides*, *Zea mays* and *Vigna unguiculata*, immature seeds of each being used. Diets other than mature cotton seeds are less suitable for breeding, as judged by fecundity of females and development of nymphs, but the influence of nymphal diet on adult fecundity is not consistent. Females reared on sorghum are smaller than those reared on cotton seed and they may lay fewer eggs.

There is an indication that varieties of sorghum may differ in their suitability for producing maximum fecundity and fertility. Those varieties to which the stainer exhibits a predisposition in the field may not be the most suitable.

When adults are fed on cotton bolls of ages 1–10 weeks, the fecundity of females, and the rate of egg-production increase with increasing age of boll, and the preoviposition period decreases.

Stored cotton seed may be less suitable for egg-production than freshly harvested seed cotton.

Extraction of oil from cotton seed with petroleum ether does not wholly impair the fecundity rate of females fed on the seed, but may reduce the fertility and nymphal survival in the first instar.

A diet of cotton seed, heat treated at 150–190°C. for one hour, reduces the fecundity in the females, possibly by destroying the accessory food factors. Nymphal survival is possible on such treated seed, but not when thus heated for two hours at or above 150°C.

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References.

- BAILLIE, A. F. H. (1953). Entomology.—*Progr. Rep. Exp. Stas Emp. Cott. Gr. Corp. 1951–1952* N. Nigeria pp. 11–25.
- BEBBINGTON, A. G. & ALLAN, W. (1936). Northern Rhodesia. Research Station, Mazabuka. Progress report on the cotton work, season 1934–35.—*Progr. Rep. Exp. Stas Emp. Cott. Gr. Corp. 1934–1935* pp. 61–67.
- CREIGHTON, J. T. (1938). Factors influencing insect abundance.—*J. econ. Ent.* **31** pp. 735–739.
- DAHMS, R. G., SNELLING, R. O. & FENTON, F. A. (1936). Effect of several varieties of sorghum and other host plants on biology of the chinch bug.—*J. econ. Ent.* **29** pp. 1147–1153.
- FRAENKEL, G. & BLEWETT, M. (1946). Linoleic acid, vitamin E and other fat-soluble substances in the nutrition of certain insects, *Ephestia kuehniella*, *E. elutella*, *E. cautella* and *Plodia interpunctella* (Lep.).—*J. exp. Biol.* **22** pp. 172–190.
- FRIEND, W. G. (1958). Nutritional requirements of phytophagous insects.—*Annu. Rev. Ent.* **3** pp. 57–74.
- GEERING, Q. A. (1953). A cotton stainer (*Dysdercus supersticiosus* Fabr.) as a potential pest of sorghum.—*Emp. J. exp. Agric.* **20** pp. 234–239.
- GEERING, Q. A. (1956). A method for controlled breeding of cotton stainers, *Dysdercus* spp. (Pyrrhocoridae).—*Bull. ent. Res.* **46** pp. 743–746.
- HADDOW, A. J. (1960). Studies on the biting habits and medical importance of East African mosquitos in the genus *Aedes*. I.—*Bull. ent. Res.* **50** pp. 759–779.
- HARRIS, P. L., QUAIFFE, M. L. & SWANSON, W. J. (1950). Vitamin E content of foods.—*J. Nutr.* **40** pp. 367–381.
- HILDITCH, T. P. (1947). The chemical constitution of natural fats.—2nd edn., 553 pp. London, Chapman & Hall; New York, Wiley.
- MILNE, A. (1959). Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). VI. The flight season: reproductive state of females.—*Bull. ent. Res.* **50** pp. 467–486.
- MILNE, A. & LAUGHLIN, R. (1956). Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). I. The adult and egg production.—*Bull. ent. Res.* **47** pp. 7–22.

- PEARSON, E. O. (1934). Preliminary observations on cotton stainers and internal boll disease of cotton in S. Africa.—*Bull. ent. Res.* **25** pp. 383–414.
- PEARSON, E. O. (1937). Investigations on cotton stainers and internal boll disease.—*Progr. Rep. Exp. Stas Emp. Cott. Gr. Corp.* 1935–36 pp. 37–42.
- RAINEY, R. C. (1948). Observations on the development of the cotton boll, with particular reference to changes in susceptibility to pests and diseases.—*Ann. appl. Biol.* **35** pp. 64–83.
- RAW, F. (1951). The ecology of the garden chafer, *Phyllopertha horticola* (L.) with preliminary observations on control measures.—*Bull. ent. Res.* **42** pp. 605–646.
- TRAGER, W. (1947). Insect nutrition.—*Biol. Rev.* **22** pp. 148–177.
- TROUVELOT, B. & GRISON, P. (1935). Variations de fécondité du *Leptinotarsa decemlineata* Say avec les *Solanum* tubifères consommés par l'insecte.—*C. R. Acad. Sci., Paris*, **201** pp. 1053–1055.
- Wigglesworth, V. B. (1950). The principles of insect physiology.—4th edn., 544 pp. London, Methuen; New York, Dutton.

THE SWAMP-BREEDING MOSQUITOS OF UGANDA: RECORDS OF LARVAE AND THEIR HABITATS.

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In Uganda there are some 2,500 sq. miles of permanent swamps and probably as much of seasonal swamps which develop in the rainy season (L. C. Beadle & E. M. Lind, Research on the swamps of Uganda. Unpublished MS.). The swamps are extremely varied in their distribution, extent and nature (Hancock, 1930, 1934; Hopkins, 1940; Beadle, 1954, 1957, 1958; Beadle & Lind, *op. cit.*; Carter, 1955; Lind, 1956). They may be distinguished as permanent or seasonal; or as composed principally of grass, papyrus, or sphagnum; or as occurring at lake-edges, in rivers, or inland valleys, or at high or low altitude. Moreover they may undergo considerable alteration by human interference. Thus, as Goma (1958) has pointed out, the swamp environment is not a uniform one and it provides a variety of conditions for the breeding of mosquitos.

Some 246 species, subspecies and varieties of mosquitos are known to occur in Uganda. Of these, 92 (37.4%) have been recorded breeding in the various swamps. However, the number of species that breed exclusively in the swamps is very small. Only 26 species (10.6%) of the total known Uganda mosquitos have not been recorded outside swamps.

The majority of swamp-breeding mosquitos in Uganda are Culicines, the Anophelines comprising only 21.7 per cent. *Anopheles symesi* Edw., a species not considered to be of any importance as a vector of malaria because of its rarity, is the only Anopheline mosquito that has not been recorded breeding outside swamps (Evans, 1938; De Meillon, 1947).

Certain species appear to be more or less confined to certain types of swamp. For example, *Anopheles kingi* Christ., *A. marshalli* var. *gibbinsi* Evans, *A. christyi* (Newst. & Cart.) and *Culex* (*Culex*) *ninagongoensis* Edw. have been recorded only from high-altitude swamps. Those species which have a marked preference for moderately clean water occur more frequently in lake-edge swamps, e.g., *Mansonia* (*Mansonioides*) *africana* (Theo.), and in river swamps (like those fringing the Victoria and Albert Niles), e.g., *C. (C.) poicilipes* (Theo.) and *Ficalbia* (*Mimomyia*) *splendens* (Theo.). Other species are most frequent in papyrus swamps, especially in extremely deoxygenated water containing rotting vegetation and varying amounts of reddish-brown flocculence and with light to heavy iridescent ferruginous surface scums, e.g., *C. (Neoculex) rubinotus* Theo., *Hodgesia cyptopus* Theo. and *Uranotaenia pallidocephala* Theo. Still other species are much more widespread, e.g., *C. (Lutzia) tigripes* Grp. and *C. (C.) annulioris* Theo., the breeding places of the former being limited more by the presence or absence of other mosquito larvae on which to prey than by any other factor, while those of the latter are governed by the presence of filamentous green algae (Hopkins, 1952; Goma, *op. cit.*).

There is a definite zonal distribution of some mosquitos within a swamp. For example, *C. (C.) grahami* Theo., *C. (C.) guiarti* Blanch. and *F. (Ficalbia) malfeyti* Newst. occur only in peripheral zones (Goma, *op. cit.*). In general, the interior of the large swamps is unfavourable to the breeding of Anophelines; but Culicines are very abundant there. Also, peripheral zones, especially in natural untouched

swamps, are much more productive than the interior (Goma, *op. cit.*). The ecological basis of zonal distribution is not clearly known. The high degree of organic pollution of the water derived from decaying papyrus and other vegetation, which obtains in the interior of papyrus swamps, might account for the absence of Anophelines there (Hopkins, 1940). The deliberate pollution of Anopheline breeding places is now a well-known naturalistic method of control (Muirhead-Thomson, 1951).

Swamp-breeding mosquitos are profoundly affected when swamps are altered by human interference, which takes various forms. For example, reclamation of swamps may involve afforestation, drainage, clearing and cultivation, while cutting and burning of papyrus and other swamp plants is a common practice (Goma, *op. cit.*). Agricultural operations, especially the uncontrolled cultivation of sweet potatoes in swampy land, are liable to lead to troublesome breeding of mosquito larvae (Uganda, 1950). In parts of Kigezi District, cultivation of swamps resulted in increased production of *Anopheles christyi*, while the larval populations of *A. marshalli* var. *gibbinsi* decreased greatly (Steyn, 1946). Namanve Swamp near Kampala was originally almost entirely free from larvae of *A. gambiae* Giles and it was only when reclamation began that conditions became suitable for this species (Hancock, 1934). In the Eastern Province, the growing of rice in the swamps fringing Lake Kioga was a prolific source of *A. gambiae* (Uganda, 1950).

In general, swamps that have been artificially disturbed, particularly by cultivation, cutting and trampling down of vegetation, produce more mosquito larvae than do natural untouched swamps. But, when swamps have been altered by burning of papyrus and other vegetation, there is an inhibition of breeding which lasts until the plants are almost fully regenerated (*i.e.*, up to some four or five months); on the other hand the stimulating effect of cutting falls off much earlier (Goma, *op. cit.*).

A point of practical importance is the relation between swamps and mosquito-borne diseases. For a long time the belief has been held that the high incidence of malaria in Uganda was due to the presence of extensive swamps, in which the vector species were presumed to breed. This would seem to be erroneous. Neither *A. gambiae* nor *A. funestus* Giles, the principal vectors of malaria in most parts of the country, normally breeds extensively in the swamps (Hopkins, 1940). There is danger, however, if swamps are interfered with, as has been pointed out above. In Kigezi District, it was clearly shown that the increased incidence of malaria there was directly due to the cultivation of swamps, which made breeding conditions more favourable for Anophelines (Steyn, *op. cit.*). The yellow-fever mosquitos, *Aedes* (*Stegomyia*) *aegypti* (L.) and its near relatives, do not breed in swamps at all. But the majority of *Mansonia* species, some of which are known to be important vectors of filariasis, are common swamp breeders. On the whole, from the point of view of human disease, the swamps of Uganda would, therefore, appear to be not as dangerous as previously thought.

The species: records of occurrence and habitat of larvae.

The following list of the swamp-breeding mosquitos of Uganda deals exclusively with larvae. The records and accompanying notes, presented in a very condensed form in the interests of economy of space, have been compiled both from the literature and from the author's own personal observations, covering a period of almost three and a half years since 1955. The author has made collections of larvae from all the districts and his studies have covered practically all the various types of swamp outlined above. Only 58 species have been recorded in the present studies. The list includes six new swamp records, and also 14 unrecognised and probably undescribed swamp-breeding species.

In certain cases, published records have had to be rejected, because their

authors did not definitely state whether these were based on larvae or on adults. Also, one or two swamp records by Hopkins (Evans, 1938; Hopkins, 1952) have been included in the present list on the assumption that they refer to Uganda, although he does not definitely state that this is so. The assumption is based mainly on the facts that much of what Hopkins states in his book is from his own personal observations in Uganda, and that the mosquitos concerned occur in this country. In all cases in which the present author is unable personally to confirm a record, a reference to the authority is given, and where there is no previous record, as far as he is aware, the information is shown as a new swamp record.

1. *Anopheles (Anopheles) coustani* Lav.

Lake-shore, river and inland valley swamps; grass, papyrus and sphagnum swamps; high- and low-altitude swamps. The species will tolerate a very wide range of swamp conditions; pools in virgin, cut and burnt papyrus; in cut and virgin *Miscanthidium* and slashed *Phoenix* (Hancock, 1934); in both cultivated and uncultivated swamps (Steyn, 1946); edges of swamps where cultivation ends (Hancock, 1930); or considerable distances inside papyrus swamps. Open pools, or among *Azolla*, *Ceratophyllum*, *Lemna* and *Pistia*. Water, clean or foul and containing reddish-brown flocculence and with light to heavy iridescent ferruginous surface scums.

2. *A. (A.) symesi* Edw.

In dense papyrus swamps on the northern shore of Lake Victoria (Evans, 1938). Not recorded outside swamps.

3. *A. (A.) implexus* (Theo.).

Larvae occur under very heavy tree shade. Peripheral zones of a papyrus swamp; a mixed grass-papyrus swamp, water fairly clear but containing brown flocculence at the bottom. In dense shade at edges of a swamp and in more open swamps (Hancock, 1930). In slashed and true *Phoenix* swamps (Hancock, 1934).

4. *A. (Myzomyia) kingi* Christ.

A high-altitude species. Abandoned, previously cultivated, sedge swamps, in pools with 'soft' bottom, and in some cases larvae were found on the surface of extremely black 'muddy soup', temperature 15°C., altitude 6,600-6,700 ft., Kigezi District. A small swamp at 7,000 ft. on Mt. Elgon, temperature 13°C. (Hancock & Soundy, 1931).

5. *A. (M.) funestus* Giles.

The species does not normally breed intensively in the swamps (Hopkins, 1940) and is seldom found in the many papyrus swamps (Leeson, 1937). There is, however, a considerable amount of breeding in the zone at the land edge of papyrus swamps, but the species extends only a very short distance into the papyrus zone (Hopkins, 1940). Lake-shore swamps, in papyrus growing in clear water (Leeson, *op. cit.*; Garnham, Wilson & Wilson, 1948). Grass swamps provide more favourable breeding places, especially if the grass is not tall (Hopkins, 1940). Edges of swamps where cultivation ends (Hancock, 1930). River swamps fringing the Victoria and Albert Niles, in grass zones and among *Pistia* and *Ceratophyllum*.

6. *A. (M.) rivulorum* Leeson.

No definite previous swamp record. River swamps fringing the Albert Nile, in grass zone and among *Pistia* and *Ceratophyllum*, at Dufile, Laropi and Laropi Port, West Nile District.

7. *A. (M.) rivulorum* var. *garnhamellus* Evans & Leeson.

River swamps fringing the Victoria Nile at Atura, and the Albert Nile at Laropi, Rhino Camp and Pakwach, and in a swamp pool near Arua (Leeson, 1937). This form is not regarded as a distinct variety by De Meillon (1947).

8. *A. (M.) marshallii* (Theo.).

Swampy valleys (Uganda, 1933). High-altitude papyrus swamp, at about 5,500 ft., at Nsika, Ankole District.

9. *A. (M.) marshallii* var. *gibbinsi* Evans.

A high-altitude form. Papyrus swamp at about 5,500 ft., at Nsika, Ankole District. Mixed swamp dominated by papyrus, *Cladium* and *Phragmites*, near Fort Portal, Toro District; pools where these plants had recently been burnt, water very flocculent and temperature 17°C. In Kigezi District, Steyn (1946) found that larvae of this species were more frequent in untouched than in cultivated swamps. In untouched swamp breeding places, oily scums, iron hydroxide flocculence and decayed vegetation are often present. Not recorded outside swamps.

10. *A. (M.) moucheti* Evans.

Namanve Swamp, in the fringing papyrus at the lakeward side of the swamp (Hancock, 1934).

11. *A. (M.) hancocki* Edw.

Swampy valleys (Uganda, 1933).

12. *A. (M.) theileri* Edw.

Edges of swamps where cultivation ends (Hancock, 1930).

13. *A. (M.) wellcomei wellcomei* Theo. (= *distinctus* var. *ugandae* Evans).

Larvae were taken from clumps of short grass growing through clear water on the outer edge of Nakasenji Swamp, Jinja (Gillett, 1955).

14. *A. (M.) demeilloni* Evans.

Swamps are included among its various breeding places (Evans, 1938; De Meillon, 1947).

15. *A. (M.) garnhami* Edw.

A high-altitude species. A single larva was found in a swamp in the saddle between Mt. Mgahinga and Mt. Sabinio, at about 8,000 ft., Kigezi District (Edwards & Gibbins, 1939).

16. *A. (M.) christyi* (Newst. & Cart.).

A high-altitude species. Steyn (1946) found that the species was relatively more common in cultivated than in untouched swamps. It bred intensively in cultivated swamps and generally disappeared when neglected areas reverted to swamp. Individual breeding places that were negative for this species in untouched swamps produced it subsequent to cultivation. It bred where papyrus had been cut down, but tended to disappear as the papyrus regenerated.

17. *A. (M.) gambiae* Giles.

Like *A. funestus*, *A. gambiae* does not normally breed intensively in the swamps (Hopkins, 1940) and breeding is definitely less extensive than in the

former species. It does not normally breed in swamps away from the margins, where it occurs chiefly in disturbed vegetation. It disappears immediately one enters the papyrus zone (Hopkins, 1940). Edges of swamps where cultivation ends (Hancock, 1930). In Bwamba County, larvae were found in swampy patches of highly saline tepid water from hot springs, temperature 30.5–38°C.; water scummy and with a very strong smell of sulphur. Haddow & others (1951) recorded the species in similar places from this area. Human interference has at times made swamps more favourable for the breeding of this species (Hancock, 1934; Uganda, 1950).

We are investigating whether the absence of larvae of *A. gambiae* from the interior of swamps is due to the fact that no eggs are laid there by the female mosquito, or, alternatively, to the fact that, although the female may oviposit indiscriminately, the eggs and/or larvae cannot develop in the interior of the swamp. There is some evidence that the conditions in the interior of papyrus swamps are unfavourable for the early larval stages. Hancock (1934) suggests that there is an absence of larval food in swamp waters.

18. *A. (M.) maculipalpis* (Giles).

Swamps (Evans, 1938) and swampy valleys (Uganda, 1938).

19. *A. (M.) pharoensis* Theo.

Lake-shore swamps, in clear water, among *Pistia* and *Ceratophyllum*. An inland swamp covered with floating vegetation (Evans, 1938).

20. *A. (M.) squamosus* Theo.

Lake-shore swamps, in clear water, among *Ceratophyllum*. Edges of swamps where cultivation ends (Hancock, 1930). At edges of swamps in clear water (Evans, 1938).

21. *Hodgesia sanguinea* Theo.

A typical swamp-breeding species. Pools in virgin papyrus and virgin *Miscanthidium* swamps, and among fern in the vegetational zone at the lakeward end of Namanve Swamp (Hancock, 1934). Small pools of dark-coloured water in papyrus swamp; some of these pools had a pH as low as 4.4 (Hopkins, 1952).

22. *H. cytopus* Theo.

Grass and papyrus swamps and the river swamps fringing the Albert Nile. A common inhabitant of the interior of papyrus swamps. In virgin *Miscanthidium*, virgin, cut, burnt, and completely regenerated papyrus areas. Rank vegetation or fairly open water, invariably covered with iridescent ferruginous surface scums and containing heavy reddish-brown flocculence and a lot of decaying organic matter. Highest productivity occurs in recently burnt papyrus habitats (Goma, 1958). Not recorded outside swamps.

Some unusual larvae of this species were sent to Mrs. van Someren, Nairobi, for examination. She found that the specimens differ from the description and from other larvae she had seen from Uganda by having the lateral seta simple, not barbed (personal communication).

23. *Uranotaenia pallidocephala* Theo.

A typical swamp-breeding species. Grass, papyrus and mixed grass-papyrus swamps. Most frequent inside papyrus swamps. In virgin, cut, burnt, and completely regenerated papyrus areas. Water most often with light to heavy

A12
iridescent ferruginous surface scums and containing reddish-brown flocculence and much rotting vegetation. A papyrus swamp at about 4,580 ft., temperature 16°C., Toro District. Pools in *Phoenix* swamp and among fern in the vegetational zone at the lakeward end of Namanve Swamp (Hancock, 1934).

24. *U. alboabdominalis* Theo.

Pools in virgin *Miscanthidium*, virgin papyrus, and slashed *Phoenix* swamps (Hancock, 1934).

25. *U. balfouri* Theo.

A13
Lake-shore, river and inland valley swamps, most particularly papyrus swamps. Most frequent inside papyrus swamps especially in virgin and completely regenerated papyrus habitats, in which highest larval productivity occurs (Goma, 1958). Also where papyrus has been cut or burnt. In the swamps fringing Lake Kioga the species breeds in a floating 'lawn' of the grass, *Leersia hexandra*, just before the fern zone which borders on the open water. High-altitude swamps of Kigezi District; in abandoned, previously cultivated, papyrus swamps, temperature 16°C. Water clear, sometimes pools with black muddy 'soft' bottom; most often with light to heavy iridescent ferruginous surface scums and containing reddish-brown flocculence. Virgin and cut *Miscanthidium*, virgin and slashed *Phoenix* swamps (Hancock, 1934). Occurs not uncommonly in old craters filled with papyrus swamp in open patches among *Riccia* (a floating liverwort), Toro District (Hopkins, 1952).

26. *U. chorleyi* Edw.

A14
Swampy area on the shores of Lake Nabugabo, among grass; water shaded, with heavy iridescent ferruginous surface scum and containing a red flocculence. Sedge swamps (Hopkins, 1952).

27. *U. hopkinsi* Edw.

A15
Grass, papyrus and mixed grass-papyrus swamps. In recently cut papyrus areas and where the papyrus has been cut a long time previously. Water with iridescent ferruginous surface scums and containing brown flocculence. Pools in *Miscanthidium* swamp (Hancock, 1934).

28. *U. mashonaensis* Theo.

A16
Most frequent in papyrus swamps. In virgin, cut, burnt, and completely regenerated papyrus areas. Highest productivity occurs in virgin and completely regenerated papyrus habitats (Goma, 1958). In the high-altitude swamps of Kigezi District the species breeds inside swamps in trampled and previously cut papyrus areas and in abandoned, previously cultivated, papyrus swamps, temperature 16.5-17°C. Water invariably with iridescent ferruginous surface scums and containing brown flocculence. Pools in virgin *Miscanthidium* swamp (Hancock, 1934); and the more open parts of papyrus swamp occupying an old crater, where larvae were found among *Lemna* (Hopkins, 1952). Not recorded outside swamps.

29. *Aëdomyia africana* Nev.-Lem.

A17
Most frequent in lake-shore swamps (Hancock, 1930; Hopkins, 1952) and less so in the river swamps fringing the Albert Nile, in clear water among *Pistia* and *Ceratophyllum*. Once found breeding in very foul water in a grass and *Pistia* zone of a river swamp.

30. *A. furfurea* End.

In swamps as *A. africana* (Hopkins, 1952). In an inland papyrus swamp, in peripheral zone, among sedge and other grasses, in shallow water containing very heavy darkish-brown flocculence.

31. *Ficalbia (Mimomyia) splendens* (Theo.).

Lake-shore swamps and the river swamps fringing the Albert Nile, invariably among *Pistia* and *Ceratophyllum*, in clear water. Larvae have also been found breeding in turbid, extremely deoxygenated water with very black muddy 'soft' bottom, and in foul-smelling water in grass and *Pistia* zone of river swamps.

32. *F. (M.) hispida* (Theo.).

Most frequent in papyrus swamps; in virgin, cut, burnt, and completely regenerated papyrus areas. In the high-altitude swamps of Kigezi District, larvae occur in abandoned, previously cultivated, papyrus swamps, temperature 16–18°C. Highest larval productivity occurs in recently cut papyrus areas (Goma, 1958). Pools in virgin *Miscanthidium* swamp (Hancock, 1934). Water with iridescent light to heavy ferruginous surface scums and containing brown flocculence.

33. *F. (M.) hispida* var. *sunyaniensis* Edw.

No definite previous swamp record. Papyrus swamp fringing the Kazinga Channel, at about 3,000 ft.; in recently cut papyrus area. Water flocculent and with an iridescent ferruginous surface scum; temperature 23°C.

34. *F. (M.) lacustris* Edw.

Lake-shore, river, and inland valley swamps; grass and papyrus swamps. Common among short grass and other vegetation at inner edge of swamps bordering Lake Victoria (Hopkins, 1952). In lake-shore swamps water often clear; but in inland papyrus swamps, with ferruginous surface scums and containing brown flocculence. Not recorded outside swamps.

35. *F. (M.) perplexans* Edw.

Among grass in a river swamp fringing the Albert Nile. Swamp pools (Hopkins, 1952).

36. *F. (M.) pallida* Edw.

New swamp record. River swamps fringing the Albert Nile at Dufile and Laropi, West Nile District. Among *Pistia*, both at the inner swamp edge where the water was clean and at the land edge in extremely deoxygenated water, with very black muddy 'soft' bottom and plenty of débris on the surface.

37. *F. (M.) mimomyiaformis* (Newst.).

River swamps fringing the Albert Nile; in clear water, among *Pistia* and *Ceratophyllum*. Pools in *Miscanthidium* swamp (Hancock, 1934) and at margins of swamps, always among vegetation and always in clear water (Hopkins, 1952).

38. *F. (M.) mimomyiaformis* var. *pincerna* (Graham).

Pools at margins of swamps, always among vegetation and always in clear water (Hopkins, 1952).

39. *F. (M.) plumosa* (Theo.).

Papyrus swamps, inside as well as in peripheral zones; in virgin, trodden, and recently cut papyrus areas. Occurs in high-altitude swamps in water with

temperatures down to 18°C. Water always with iridescent ferruginous surface scums and containing brown flocculence. Most frequent in situations with heavy organic ooze. *Miscanthidium* swamp (Hancock, 1934) and edges of marshes (Hopkins, 1952).

40. *F. (Etorleptomyia) mediolineata* (Theo.).

Most frequent inside papyrus swamps, both in virgin and cut papyrus areas. Pools in cut *Miscanthidium* swamp (Hancock, 1934). Water with iridescent ferruginous surface scums and containing brown flocculence. In a river swamp fringing the Victoria Nile at Atura, larvae were found in turbid water with a thin oily film on the surface, probably from exhaust oil of the ferry.

41. *F. (Ficalbia) uniformis* (Theo.).

Not uncommon in lake-shore swamps, among grass, fern (Hancock, 1934; Hopkins, 1952) and *Azolla*; and in the river swamps fringing the Victoria and Albert Niles, among grass, *Pistia* and *Ceratophyllum*. Pools in cut *Miscanthidium* swamp (Hancock, 1934). Water clear, but may frequently be very foul and deoxygenated. In a river swamp fringing the Victoria Nile at Atura, larvae were found in turbid water with a thin oily film on the surface, probably from exhaust oil of the ferry.

42. *F. (F.) malfeyti* Newst.

Like *F. uniformis*, not uncommon in lake-shore swamps, among grass (Hopkins, 1952) and *Azolla*; and in the river swamps fringing the Albert Nile, among grass and *Pistia*. Highest productivity occurs in peripheral zones in permanent and semi-permanent swamp pools (Goma, 1958). Water clear to very turbid, foul and very deoxygenated. Not recorded outside swamps.

43. *Mansonia (Coquillettidia) metallica* (Theo.).

Shallow grassy swamps (Gillett, 1946) and peripheral zones in papyrus and mixed grass-papyrus swamps, in foul water. Not recorded outside swamps.

44. *M. (C.) versicolor* (Edw.).

Shallow swamps containing aquatic vegetation (Gillett, 1946). Papyrus and mixed grass-papyrus swamps, somewhat rare. Not recorded outside swamps.

45. *M. (C.) cristata* (Theo.).

A small shallow seepage swamp overgrown with semi-aquatic vegetation (Hopkins, 1952). Not recorded outside swamps.

46. *M. (C.) fuscopennata* (Theo.).

Swamps dominated by Cyperaceae, or "muddy swamps" (Hancock, 1930). Grass swamp (Gillett, 1946) and papyrus swamps, in virgin and completely regenerated papyrus areas. Not recorded outside swamps.

47. *M. (C.) aurites* (Theo.).

Shallow grassy swamps (Gillett, 1946). In foul water in swamps (Hopkins, 1952).

48. *M. (C.) microannulata* (Theo.).

Shallow grassy swamps (Gillett, 1946) and in a large papyrus swamp where the water contained much rotting vegetation (Hopkins, 1952). Not recorded outside swamps.

49. *M. (C.) fraseri* (Theo.).

A shallow grassy swamp in dense forest (Gillett, 1946, 1949). Not recorded outside swamps.

50. *M. (Mansonioides) africana* (Theo.).

Has a marked preference for moderately clean water and is therefore somewhat more frequent in lake-shore swamps (Hancock, 1930; Hopkins, 1952) and the river swamps fringing the Albert Nile. In inland papyrus swamps, larvae occur in both virgin and completely regenerated papyrus areas. Not recorded outside swamps.

51. *M. (M.) uniformis* (Theo.).

Larger swamps, especially lake-shore swamps (Hopkins, 1952). River swamps fringing the Albert Nile, among grass, *Pistia* and *Ceratophyllum*, in both clean and turbid water. In inland papyrus swamps larvae occur in virgin, recently and previously cut papyrus and completely regenerated papyrus areas.

52. *Aedes (Mucidus) mucidus* (Karsch).

Pools in papyrus swamp burnt earlier and in both untouched and slashed *Phoenix* swamps (Hancock, 1934). Not recorded outside swamps.

53. *A. (Aedimorphus) punctothoracis* (Theo.).

Pools in *Phoenix* swamp (Hancock, 1934).

54. *A. (A.) domesticus* (Theo.).

Grass swamp; pools containing *Sagittaria*, *Sphagnum* and filamentous green algae and fringed with fern; at periphery of swamp. Pools in papyrus swamp burnt earlier, in virgin *Miscanthidium*, and in untouched and slashed *Phoenix* swamps (Hancock, 1934). Small pools in a grassy swamp (Hopkins, 1952). Not recorded outside swamps.

55. *A. (A.) tarsalis* (Newst.).

Pools among grass and papyrus inside a lake-shore swamp. Pools in virgin and cut *Miscanthidium*, virgin and previously burnt papyrus, and untouched and slashed *Phoenix* swamps (Hancock, 1934).

56. *A. (A.) albocephalus* (Theo.).

Typical breeding sites are grassy swamps (Hopkins, 1952). Pools in slashed *Phoenix* swamp and papyrus swamp burnt earlier (Hancock, 1934). A high-altitude grassy swamp bordering Lake Mutanda, in shallow clear water, temperature 21.5–23°C. Not recorded outside swamps.

57. *A. (A.) alboventralis* (Theo.).

Not uncommon in open pools in swampy ground (Hopkins, 1952). Not recorded outside swamps.

58. *A. (A.) gibbinsi* Edw.

Numerous larvae in a swamp in the saddle between Mt. Mgahinga and Mt. Sabinio, Kigezi District, at about 8,000 ft. (Edwards & Gibbins, 1939). Ditches in an abandoned, previously cultivated, papyrus swamp on the shores of Lake Mutanda, Kigezi District, temperature 17.5°C., altitude about 5,880 ft.

59. *A. (A.) quasiunivittatus* (Theo.).

New swamp record. High-altitude papyrus swamps, Kigezi District. Pools in dense papyrus swamp choking Ruhezaminda River and ditches overgrown with grass, in an abandoned previously cultivated papyrus swamp on the shores of Lake Mutanda, temperature 16°C.

60. *A. (A.) dentatus* (Theo.).

Often common after heavy rains at edges of swamps (Hopkins, 1952). Among grass in clear, shallow water at swampy edge of Lake Mutanda and in ditches overgrown with grass in an abandoned, previously cultivated, papyrus swamp, on the shores of the same lake, Kigezi District. Numerous larvae in a rather open temporary swamp at Kanaba Gap and (?) in a swamp in the saddle between Mt. Mgahinga and Mt. Sabinio, Kigezi District (Edwards & Gibbins, 1939).

61. *A. (Neomelaniconion) lineatopennis* (Ludl.).

Grass and papyrus swamps, both in virgin and cut papyrus areas. In the high-altitude swamps of Kigezi District, larvae in abandoned, previously cultivated, papyrus swamps. Virgin and cut *Miscanthidium*, untouched and slashed *Phoenix* swamps and in papyrus swamps burnt earlier (Hancock, 1934). Commonest in pools at edges of swamps (Hopkins, 1952).

62. *A. (N.) circumluteolus* (Theo.).

The larvae and breeding places of this species appear to be absolutely indistinguishable from those of *A. (N.) lineatopennis* (Hopkins, 1952). We find this to be so in the present studies.

63. *Culex (Lutzia) tigripes* Grp.

Common in swamps, more particularly papyrus swamps; in virgin, cut, burnt and regenerated papyrus areas. A papyrus swamp at about 4,580 ft., temperature 16°C., Toro District. In the high-altitude swamps of Kigezi District, larvae occur in abandoned, previously cultivated, papyrus swamps, temperature 16-18.5°C. Highest larval productivity occurs in recently burnt papyrus areas (Goma, 1958). Both virgin and altered *Miscanthidium* and *Phoenix* swamps (Hancock, 1934). However, the breeding places of this species seem to be limited more by the presence or absence of other mosquito larvae on which to prey than by any other factor (Hopkins, 1952). Water invariably with light to heavy iridescent ferruginous surface scums and containing brown flocculence.

64. *C. (Neoculex) andreanus* Edw.

Pools in virgin *Miscanthidium*, untouched and slashed *Phoenix* swamps (Hancock, 1934). Pools among tall papyrus and 'makindu' palms (*Phoenix reclinata*) (Hopkins, 1952). Not recorded outside swamps.

65. *C. (N.) kingianus* Edw.

Pools in virgin and slashed *Phoenix* and virgin *Miscanthidium* swamps; papyrus swamp burnt earlier (Hancock, 1934).

66. *C. (N.) rubinotus* Theo.

A most regular inhabitant of swamps, particularly inside papyrus swamps. Grass and papyrus swamps, at both high and low altitudes. Very rare in the river swamps fringing the Victoria and Albert Niles. In papyrus swamps it breeds in virgin, cut, burnt, and completely regenerated papyrus areas. Highest larval

productivity occurs in recently cut papyrus habitats (Goma, 1958). Pools in a papyrus swamp at about 4,580 ft., temperature 16°C., Toro District. In the high-altitude swamps of Kigezi District, larvae have been found breeding in (a) pools in a mixed fern-*Typha*-sedge-papyrus swamp, temperature 13°C., (b) pools in dense papyrus swamp, temperature 16.5°C., (c) pools in abandoned, previously cultivated, papyrus swamp, temperature 16-17.5°C., and (d) pools in virgin, cut, and regenerated papyrus swamps, temperature 17-18°C. The species can thus tolerate a wide range of temperature. Virgin and slashed *Phoenix*, virgin and altered *Miscanthidium* and papyrus swamps (Hancock, 1934). Water in the various breeding places invariably with iridescent ferruginous surface scums and containing brown flocculence.

67. *C. (N.) insignis* (Cart.).

A larva was taken from a swamp at Musoli, Entebbe (van Someren, 1956). Not recorded outside swamps.

68. *C. (Culicomyia) semibrunneus* Edw.

Pools in slashed *Phoenix* swamp (Hancock, 1934). Pools among tall papyrus and 'makindu' palms (*Phoenix reclinata*) (Hopkins, 1952). Larvae from a swamp at Zika near Entebbe (van Someren, 1956). Not recorded outside swamps.

69. *C. (Culex) poicilipes* (Theo.).

Has a marked preference for clean water and is, therefore, more frequent in lake-shore swamps and the river swamps fringing the Victoria and Albert Niles, invariably among *Pistia* and *Ceratophyllum*. Occasionally larvae breed in very foul and extremely deoxygenated swamp water. At Atura, larvae were found in turbid water with a thin oily film on the surface, probably from exhaust oil of the ferry. In the swamp fringing Lake Bunyonyi, where it connects with the Ruhuma River, larvae were scanty among green filamentous algae in the *Typha*-papyrus zone, temperature 20°C. Slashed *Phoenix* swamp (Hancock, 1934).

70. *C. (C.) bitaeniorhynchus* Giles.

Grass and papyrus swamps, at both high and low altitudes. At edges, invariably among filamentous green algae. Pools in virgin and completely regenerated papyrus swamps. In Kigezi District, in both virgin and abandoned, previously cultivated, sedge swamps, among filamentous green algae and *Utricularia*; occasionally larvae occur on surface of 'muddy soup', especially in pools with muddy 'soft' bottom; temperature may be as low as 15°C. Papyrus swamps fringing Lake Bunyonyi (Garnham, Wilson & Wilson, 1948).

71. *C. (C.) ethiopicus* Edw.

Sedge swamp near Lake Bunyonyi; in neglected, previously cultivated, swamp; scummy pools with muddy 'soft' bottom; occasionally larvae on surface of 'muddy soup'; temperature may be as low as 15°C. The larvae of *C. ethiopicus* and *C. bitaeniorhynchus* are extremely similar and the recorded breeding places of the one are probably also those of the other.

72. *C. (C.) aurantapez* Edw.

Swamps bordering Lake Victoria (Hopkins, 1952). *Miscanthidium*, papyrus and *Phoenix* swamps; in cut *Miscanthidium*, and in virgin and burnt (earlier) papyrus areas (Hancock, 1934).

73. *C. (C.) annulioris* Theo.

Grass and papyrus swamps, at both high and low altitudes, invariably among filamentous green algae. Highest larval productivity occurs in peripheral zones, in permanent and semi-permanent swamp pools. In Kigezi District, larvae are common in the lake-shore swamps bordering Lakes Bunyonyi and Mutanda, in clear water, among filamentous green algae and *Utricularia*, temperature 18.5–23°C. Also in abandoned, previously cultivated, papyrus swamps. *Miscanthidium*, papyrus, and *Phoenix* swamps; in cut *Miscanthidium*, and in virgin and burnt (earlier) papyrus (Hancock, 1934). The larvae of *C. annulioris* and *C. aurantapex* are extremely similar and the recorded breeding places of the one are probably also those of the other.

74. *C. (C.) duttoni* Theo.

Pools in cut *Miscanthidium* swamp (Hancock, 1934). Holes in swamps, water more commonly muddy than clear and often foul from organic matter (Hopkins, 1952). We have confirmed Hopkins' general observations. Small pools in cut papyrus swamps. In Kigezi District, overgrown ditches in abandoned, previously cultivated, papyrus swamps.

75. *C. (C.) theileri* Theo.

Pools in papyrus swamp burnt earlier (Hancock, 1934).

76. *C. (C.) univittatus* Theo.

Grass and papyrus swamps; lake-shore, river and inland valley swamps. At rank-growing edges and inside papyrus swamps, in virgin, trampled, cut, burnt, and completely regenerated papyrus areas. Highest larval productivity occurs in recently cut papyrus habitats (Goma, 1958). Untouched and slashed *Phoenix*, and virgin and cut *Miscanthidium* swamps (Hancock, 1934). Water often with iridescent ferruginous surface scums and containing brown flocculence.

77. *C. (C.) pipiens pipiens* L.

Pools at edges of swamps (Hopkins, 1952) as well as inside, in recently cut and regenerating papyrus areas. In Kigezi District, larvae breed in lake-shore swamps and in abandoned, previously cultivated, papyrus swamps. A mixed fern-*Typha*-sedge-papyrus swamp near Lake Bunyonyi, pools with temperature 13–15°C. Pools in cut and virgin *Miscanthidium* swamps (Hancock, 1934). Water clear or with iridescent ferruginous surface scums and containing brown flocculence.

78. *C. (C.) pipiens fatigans* Wied.

Pools in the edge of swamps (Hopkins, 1952).

79. *C. (C.) zombaensis* Theo.

New swamp record. A single larva found in an abandoned, previously cultivated, high-altitude papyrus swamp on the shore of Lake Mutanda, Kigezi District. Water with fairly heavy iridescent ferruginous surface scum and containing reddish-brown flocculence, temperature 17.5°C. Not recorded outside swamps.

80. *C. (C.) ninagongoensis* Edw.

A high-altitude species. Swamp in the saddle between Mt. Mgahinga and Mt. Sabinio, Kigezi District, at about 8,000 ft. (Edwards & Gibbins, 1939). Numerous larvae were found breeding in peripheral pools of the sphagnum swamp

in the crater of Mt. Mgahinga, at about 11,100 ft., temperature 10°C. No larvae were found in the interior of the swamp, where the water temperature varied from 10° to 14°C. At lower altitudes, we have recorded the species breeding in a papyrus swamp at 6,000–7,000 ft., at Nsika, Ankole District. Not recorded outside swamps.

81. *C. (C.) trifilatus* ssp. *aenescens* Edw.

Ditches in cultivated swamps (Hopkins, 1952).

82. *C. (C.) andersoni* Edw.

Swamp in the saddle between Mt. Mgahinga and Mt. Sabinio, Kigezi District, at about 8,000 ft. (Edwards & Gibbins, 1939).

83. *C. (C.) toroensis* ssp. *macrophyllus* Edw. & Gibbins.

Swamp in the saddle between Mt. Mgahinga and Mt. Sabinio, Kigezi District, at about 8,000 ft. (Edwards & Gibbins, 1939). Not recorded outside swamps.

84. *C. (C.) chorleyi* Edw.

Sedge-papyrus swamp connecting Lakes Mulehe and Mutanda, Kigezi District; in trodden footpath and in previously cut papyrus inside the swamp. Water with iridescent ferruginous surface scums and containing brown flocculence, temperature 18°C. Open pools in swamps (Hopkins, 1952).

85. *C. (C.) antennatus* (Becker).

Holes in swamps (Hancock, 1930). Abundant in swamps (Hopkins, 1952).

86. *C. (C.) quasiguiarti* Theo.

Larvae taken from a swamp at Kitinda, Entebbe (van Someren, 1956). Not recorded outside swamps.

87. *C. (C.) decens* Theo.

Papyrus and lake-shore swamps. In cut, burnt and regenerating papyrus areas. Common in the edges of swamps (Hopkins, 1952), where also highest larval productivity occurs (Goma, 1958). Water with thin iridescent ferruginous surface scums and somewhat flocculent. On the shores of Lake Kioga, larvae were found in a swamp in clear water, pH 6.8; in floating *Leersia hexandra* 'lawn' just before the fern zone bordering on the open lake water. In Kigezi District, in abandoned, previously cultivated, papyrus swamp, temperature 16°C. Cut *Miscanthidium* swamp (Hancock, 1934).

88. *C. (C.) invidiosus* Theo.

Edges of swamps (Hopkins, 1952).

89. *C. (C.) perfuscus* Edw.

New swamp record. Overgrown ditches in an abandoned, previously cultivated, high-altitude papyrus swamp, on the shores of Lake Mutanda, Kigezi District. Water with iridescent ferruginous surface scums and containing reddish-brown flocculence, temperature 16–17.5°C.

90. *C. (C.) guiarti* Blanch.

Most frequent in peripheral zones of swamps, particularly in open permanent and semi-permanent pools. Highest larval productivity occurs in such habitats

(Goma, 1958). Larvae do not occur inside swamps. In Kigezi District, larvae were found breeding among *Utricularia* in fairly clear water of a lake-shore grass swamp. Virgin and cut *Miscanthidium*, recently cut and previously burnt papyrus swamps and in slashed *Phoenix* swamps (Hancock, 1934).

91. *C. (C.) ingrami* Edw.

Somewhat uncommon in swamp pools (Hopkins, 1952).

92. *C. (C.) grahami* Theo.

Common in clear water in peripheral zones of swamps, particularly in permanent and semi-permanent pools. Highest larval productivity occurs in such habitats (Goma, 1958). Larvae do not breed inside papyrus swamps.

Notes on unrecognised and probably undescribed species.

Among the present records of mosquito larvae from the various swamps of Uganda are some fourteen species, which it has not, as yet, been possible to identify. Some of them are probably new to science. With the exception of two species, all have been obtained from high-altitude swamps.

1. *Anopheles* sp.

The larvae resemble those of *A. (Myzomyia) ardensis* (Theo.). They were found breeding in clear, rather cool, slow-flowing water, at the grassy edge of an artificial channel through a papyrus swamp, at 6,000–7,000 ft., at Nsika, Ankole District.

2. *Uranotaenia* ? *alboabdominalis* Theo.

The larvae "differ slightly from the description—the most obvious difference being that the comb teeth are more like scales than spines. They may be an undescribed species" (Mrs. van Someren, personal communication). They were found in (a) pools inside a swamp near Lake Bunyonyi, at about 6,600 ft., temperature 13°C., and (b) grass zone of river swamp fringing the Albert Nile, at Dufie, West Nile District.

3. *Aedes* (*Aedimorphus*) sp.

This larva runs down to couplet 72 of Hopkins' key (1952); but it has 4 distal pecten teeth widely spaced and, therefore, does not agree with either *A. filicis* Ingram & De Meillon or *A. mutilus* Edw. Mrs. van Someren (personal communication) thinks "they may be atypical *Ae. mutilus* or an undescribed species". A single larva, in pool in a grass swamp bordering Lake Mutanda, at about 5,880 ft.

4. *Culex* sp.

Very similar to *C. (Neoculex) salisburyensis* Theo. Larvae were found breeding in a mixed grass-papyrus swamp. Rare.

5. *Culex* sp.

Young stages. "They have unpaired tufts outside the barred area of the ventral brush, which is an unusual feature for *Culex*. As they are young stages I cannot say definitely that they are an undescribed species" (Mrs. van Someren, personal communication). Larvae were found breeding in pools in a grass swamp bordering Lake Mutanda, at about 5,880 ft.

6. *Culex* sp.

Immature larvae found in pools containing a fair amount of *Utricularia*, in a grass swamp on the shores of Lake Mutanda, temperature 19°C.

7. *Culex* sp.

Immature larvae found in the more exposed ditches overgrown with grass, in an abandoned, previously cultivated, papyrus swamp bordering Lake Mutanda, temperature 17.5°.

8. *Culex* sp.

The larvae "may be atypical *chorleyi*. . . . It is possible they might be the larvae of *C. vansomereni* ssp. ? *elgonicus* [Edw.]" (Mrs. van Someren, personal communication). Larvae were found in (a) a trodden footpath and pools in previously cut papyrus, in a mixed sedge-papyrus swamp connecting Lakes Mulehe and Mutanda, temperature 18°C., (b) pools containing *Utricularia* in a grass swamp on the shores of Lake Mutanda, temperature 19°C., and (c) overgrown ditches in an abandoned, previously cultivated, papyrus swamp bordering Lake Mutanda, temperature 17.5°C.

9. *Culex* sp.

I tentatively identified these larvae as *C. (Culex) pipiens*, but Mrs. van Someren (personal communication) remarks that they "do not appear to be typical *pipiens* and certainly at 10,000 ft. they should be *andersoni*, but they are not. The larva of *C. toroensis macrophyllus* is suspected to be like *andersoni* and it is possible that these larvae may be *macrophyllus*." Larvae were found breeding in a small swampy place on the slope of Mt. Mgahinga, Kigezi District, at about 10,000 ft., temperature 9°C., and in seepage pools a little higher up at about 10,100 ft., temperature 12°C.

10. *Culex* sp.

Mrs. van Someren (personal communication) remarks that "this is an extraordinary *Culex*. I know of nothing like it. It is very probably a new species but adults would be needed to confirm this." The larvae were found breeding in pools at the periphery and inside the sphagnum swamp in the crater of Mt. Mgahinga, at about 11,100 ft., temperature 10°C. Also in a small outflow of the swamp with extremely black muddy water, temperature 14°C. At the periphery it was associated with *C. (C.) ninagongoensis*. The species was also found in seepage pools lower down on the slope at about 10,100 ft., temperature 12°C.

11. *Culex* sp.

Larvae were found in a papyrus swamp at about 6,000 ft., at Nsika, Ankole District, at edges of a rather fast-flowing artificial channel through the swamp.

12. *Culex* sp.

Found in pools with brown surface scum and rather dark flocculent water, inside a papyrus swamp, at about 6,000 ft., at Nsika, Ankole District.

13. *Culex* sp.

Found in a papyrus swamp at 6,000-7,000 ft., at Nsika, Ankole District, at the edge of a stagnant artificial channel with a dense growth of grass.

14. *Culex* sp.

The larvae belong to the *decens* group and may possibly be *C. (C.) invidiosus* (Mrs. van Someren, personal communication). They were found among grass in the river swamps fringing the Victoria and Albert Niles. At Atura, larvae were found in turbid water with a thin oily film on the surface, probably from exhaust oil of the ferry.

Summary.

Some 246 species of mosquitos are known to occur in Uganda. Of these, 92 (37.4%) have been recorded as breeding in swamps, and the present paper brings together published data and the results of work on the collection and identification of larvae from habitats in a wide variety of types of swamp between 1955 and 1958. Notes on the occurrence and habitats of the larvae are given under each species.

In the present work, only 58 species were found breeding, but these included six new swamp records. Only 26 species appear to breed exclusively in swamps. In addition to the species identified, larvae representing some 14 unrecognised and probably undescribed species were collected. The majority of the swamp-breeding species are Culicines, the Anophelines comprising only 21.7 per cent.

The swamp environment in Uganda, with respect to the breeding of mosquitos, is extremely varied. Some possible classifications of the many and various swamps found in the country are given. The distribution of certain species of mosquitos is more or less limited to certain types of swamp. This is briefly discussed and examples are given. There is also a definite zonal distribution of some species within a swamp, e.g., *Culex (Culex) grahami* Theo., *C. (C.) guarti* Blanch. and *Ficalbia (Ficalbia) malfeyti* Newst. occur only in peripheral zones. In general, the interior of the large swamps is unfavourable to the breeding of Anophelines, but Culicines are very abundant there.

Breeding of mosquitos is profoundly affected when swamps are altered by human interference. In certain cases this has resulted in increased production of Anophelines, with the consequent aggravation of the malaria situation.

It is concluded that, from the point of view of human disease, the swamps of Uganda (especially in their natural untouched state) are not as dangerous as previously thought.

Acknowledgements.

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References.

- BEADLE, L. C. (1954). The biology of papyrus swamps.—*Publ. Cons. sci. Afr. S. Sahara* no. 6 pp. 107–111.
 BEADLE, L. C. (1957). Respiration in the African swampworm *Alma emini* Mich.—*J. exp. Biol.* **34** pp. 1–10.
 BEADLE, L. C. (1958). Hydrobiological investigations on tropical swamps.—*Verh. int. Ver. Limnol.* **13** pp. 855–857.

- CARTER, G. S. [1955]. The papyrus swamps of Uganda.—25 pp. Cambridge, Heffer.
- DE MEILLON, B. (1947). The Anophelini of the Ethiopian geographical region.—*Publ. S. Afr. Inst. med. Res.* no. 49, 272 pp.
- EDWARDS, F. W. & GIBBINS, E. G. (1939). Mosquitoes.—*Ruwenzori Exped. 1934-35* 1 no. 2 pp. 29-33. London, Brit. Mus. (Nat. Hist.).
- EVANS, A. M. (1938). Mosquitoes of the Ethiopian region. II. Anophelini, adults and early stages.—404 pp. London, Brit. Mus. (Nat. Hist.).
- GARNHAM, P. C. C., WILSON, D. B. & WILSON, M. E. (1948). Malaria in Kigezi, Uganda.—*J. trop. Med. Hyg.* **51** pp. 156-159.
- GILLETT, J. D. (1946). Notes on the subgenus *Coquillettidia* Dyar (Diptera, Culicidae).—*Bull. ent. Res.* **36** pp. 425-438.
- GILLETT, J. D. (1949). Further notes on the Ethiopian species of *Taeniorhynchus* Arribalzaga (Diptera, Culicidae).—*Proc. R. ent. Soc. Lond.* (B) **18** pp. 97-102.
- GILLETT, J. D. (1955). The male of *Anopheles* (*Myzomyia*) *distinctus* var. *ugandae* Evans (Diptera: Culicidae).—*Proc. R. ent. Soc. Lond.* (B) **24** p. 36.
- GOMA, L. K. H. (1958). The productivity of various mosquito breeding places in the swamps of Uganda.—*Bull. ent. Res.* **49** pp. 437-448.
- HADDOW, A. J., VAN SOMEREN, E. C. C., LUMSDEN, W. H. R., HARPER, J. O. & GILLETT, J. D. (1951). The mosquitoes of Bwamba County, Uganda. VIII. Records of occurrence, behaviour and habitat.—*Bull. ent. Res.* **42** pp. 207-238.
- HANCOCK, G. L. R. (1930). Some records of Uganda mosquitoes and the oecological associations of their larvae.—*Bull. Soc. R. ent. Egypte* **1930** pp. 38-56.
- HANCOCK, G. L. R. (1934). The mosquitoes of Namanve Swamp, Uganda.—*J. Anim. Ecol.* **3** pp. 204-221.
- HANCOCK, G. L. R. & SOUNDY, W. W. (1931). Notes on the fauna and flora of Northern Bugishu and Masaba (Elgon).—*J. E. Afr. Ug. nat. Hist. Soc.* no. 36 pp. 165-183.
- HOPKINS, G. H. E. (1940). Afforestation as a method of drying up swamps.—*E. Afr. med. J.* **17** pp. 189-194.
- HOPKINS, G. H. E. (1952). Mosquitoes of the Ethiopian region. I. Larval bionomics of mosquitoes and taxonomy of Culicine larvae.—2nd edn., 355 pp. London, Brit. Mus. (Nat. Hist.).
- LEESON, H. S. (1937). The mosquitos of the *funestus* series in East Africa.—*Bull. ent. Res.* **28** pp. 587-603.
- LIND, E. M. (1956). Studies in Uganda swamps.—*Uganda J.* **20** pp. 166-176.
- MUIRHEAD-THOMSON, R. C. (1951). Mosquito behaviour in relation to malaria transmission and control in the tropics.—219 pp. London, Arnold.
- VAN SOMEREN, E. C. C. (1956). Undescribed Culicine larvae and pupae from Uganda.—*Proc. R. ent. Soc. Lond.* (B) **25** pp. 3-12.
- STEYN, J. J. (1946). The effect on the Anopheline fauna of cultivation of swamps in Kigezi District, Uganda.—*E. Afr. med. J.* **23** pp. 163-169.

- UGANDA. (1933). Report of the Government Entomologist . . . during the year 1932.—*Ann. med. sanit. Rep. Uganda 1932* pp. 86-90.
- UGANDA. (1950). Malaria in the African population.—*Rep. med. Dep. Uganda 1949* pp. 13-15.

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OBSERVATIONS ON THE *SIMULIUM NEAVEI* COMPLEX AT AMANI IN TANGANYIKA.*

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Simulium neavei Roub., one of the two main vectors of human onchocerciasis in Africa, belongs to a complex of forms which occur largely in or near highland forests and, in their larval and pupal stages, attach themselves to certain fresh-water crabs (De Meillon, 1957; Freeman, 1957). Dr. M. T. Gillies, finding that one of these Simuliids was not uncommon at Amani, suggested that human onchocerciasis might exist there, and in 1957 its presence was established by Dr. M. Giaquinto (Woodman, 1958) who obtained microfilariae from some people in the hamlet of Chemka. A full understanding of the relation of Simuliids to onchocerciasis at Amani might not be of much local value but could perhaps throw light on the important practical question of the minimum number of flies which can maintain transmission. I went to Amani on 22nd October 1958 for five weeks to study the taxonomy of the local members of the *S. neavei* complex and some aspects of their biology, particularly the biting cycles of nulliparous and parous females. For this purpose captured flies were dissected and examined, and special attention was paid to the ovaries, which can furnish much information about the age of the insects and their capacity to transmit disease.

Man-biting Simuliids or human onchocerciasis has been reported from several other parts of Tanganyika by Freeman & De Meillon (1953), Gabathuler & Gabathuler (1947), Jordan (1956) and Woodman (1958). One or more members of the *S. neavei* complex occur at Kidodi, Njombe and Ubena, and probably at Mahenge; *S. damnosum* Theo. is reported from Njombe, Tukuyu and Ubena; and onchocerciasis exists at Mahenge.

Amani is 3,000 ft. above sea level on the side of the thickly wooded valley of the River Sigi which descends the eastern side of the Eastern Usambara Mountains. Moreau (1933, 1935) has pointed out some features of the area which doubtless affect the distribution of the *S. neavei* complex. The evergreen forests of the Usambaras are widely separated from any others, and this and several other mountain ranges, owing to their topography and proximity to the coast, support magnificent forest at a comparatively low altitude, in contrast to the greater part of the East African closed forest, most of which is above 3,000 ft., and some above 5,000 ft. Moreau remarked that the temperatures in the Usambaras are exceptionally low for the altitude and latitude, and that the Sigi falls so steeply—nearly 1,000 ft. in five miles near Amani—that it, as well as neighbouring streams, retains its mountain character at a lower altitude than any river elsewhere in East Africa. Crabs were collected at three points on the Sigi—upper (near Amani), middle, and lower (near Mpandeni)—which were at approximately 2,600, 1,480 and 500 ft., respectively, and in four tributary streams—an upper one at 2,700 ft., the Dodwe at 2,900 ft., the Lukungwi at 2,700 ft., and a small sluggish stream at Mpandeni. All these collecting sites are in forest country but are in or near clearings, or are exposed to the sky owing to the width of the stream.

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† Care of British Museum (Natural History).

Eight species of *Simulium* apart from the *S. neavei* complex are known to occur at Amani. A few pupae of *S. unicornutum* Pomeroy and many of *S. hirsutum* Pomeroy were taken in the Dodwe. Freeman & De Meillon (1953) reported a form of *S. debegene* De Meillon from Amani, and many of its pupae were found recently in fast water in the Sigi. With them was one pupa of *S. vorax* Pomeroy the type specimens of which were taken on a mule at Amani. Many pupae of *S. damnosum* were found in a small rapid in the Dodwe, and a few larvae at the middle point on the Sigi, but no adults were seen biting. Specimens of two species were taken in the Sigi above Mpandeni, where very few Simuliids were seen, but could not be identified; one was a pupa with eight gill filaments on a thick stem, and the other was a larva with compound hairs which were more conspicuous than those of *S. griseicollis* Becker. A species has been reported to attack birds but specimens have not been collected.

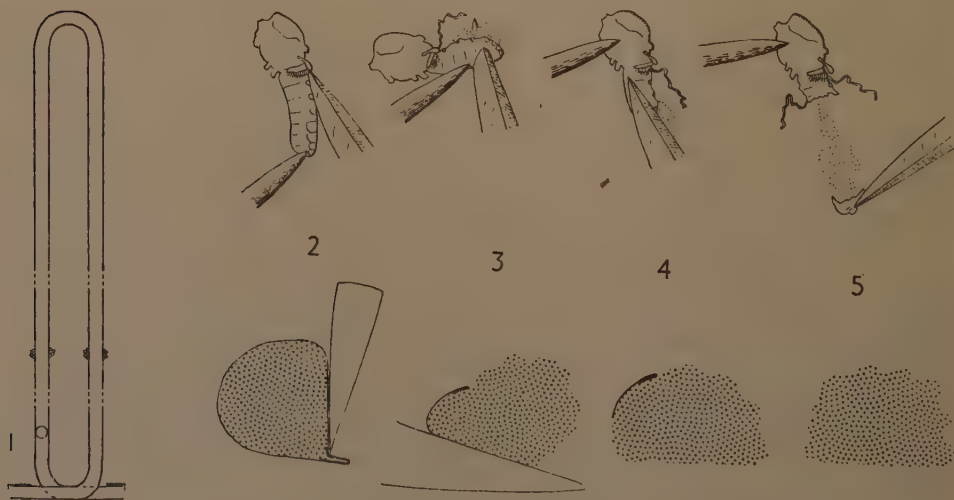
Two members of the *S. neavei* complex occur at Amani. Their systematic position cannot be decided exactly till more is known about the complex as a whole, but they have been described by Lewis (1960) as the Amani unbanded and banded forms, respectively.

Methods.

The box traps and bait traps described by McMahon, Highton & Goiny (1958) were quite useful for catching crabs at Amani, but it was usually easier to turn over the large stones which stand in shallow water, and catch the crabs by hand or drive them individually into a hand net.

At Dr. G. Pringle's suggestion, some larvae were placed in aerated jars of hay infusion for observation. Open tubes containing the larvae were dropped into the jars and many of the larvae remained in the tubes which could at any time be corked and put under a microscope. One could then identify a living larva by its submentum and watch its feeding movements and the anal hooks attached to the holdfast.

Larval skins are seldom found with pupae, but when a larva of the unbanded



Figs. 1-5.—(1) a device for measuring water speed; (2-5) diagrams of stages in the dissection of a female Simuliid, with enlarged sections of the abdomen.

form pupated in a jar it did not spin a complete cocoon, and its skin remained attached to the silk and served to identify it as the larva of this form.

A rough trial was made with a simple form of water-flow meter, mentioned by Lewis (1958a), which, unlike a Pitot tube, need not be held upright and may prove useful for measuring the flow of water on a slope or under stones where the crabs are found. It is a tube in which a relatively slow and easily measurable current is set up by the current of the stream. The meter has some resemblance to the Leon and Bentzel tubes described by Kemp (1957) and Welch (1948), and consists of a piece of glass tubing, 140 cm. long and 4 mm. wide internally, bent as shown in fig. 1 and fitted with metal clips to prevent the escape of a wax sphere. The sphere is weighted with a small piece of fine wire (driven in when hot) to give it the specific gravity of water. For calibration, a trough was made of two 12-ft. boards nailed together and caulked, one end was placed under a large tap, and the current was varied by altering the slope. The movement of a paper float was timed between markers three metres apart in the trough, and that of the sphere between elastic bands one metre from each other along the tube. When the current in the trough was 1.5 metre per second that in the tube was about a third of this, and at lower speeds the difference was greater. Before a reading was taken the sphere was moved to the starting position, and bubbles were removed from it and from the inside of the tube by holding the latter under water with its ends upward and squirting in water to which some detergent was added if the bubbles did not move readily.

Adult Simuliids were collected, while biting, in 3" \times $\frac{1}{2}$ " plastic tubes which were small enough for the flies to be easily removed. Only small numbers were taken during 12-hour catches, which were made to study biting cycles; all were dissected, and a repetition of the catches yielded an adequate total and provided additional information.

Females were dissected (figs. 2-5) in 0.9 per cent. saline in the way described by Lewis (1958a) but with one alteration. The gut tended to break when being drawn from the body, so the ventral surface of the abdomen was cut from the base towards the apex, so that some of the adherent tissues were loosened.

This method of dissection is in effect a means of peeling the integument off the abdominal viscera without damaging them, and can be done quickly so that, as in the case of Anophelines (Gillies, 1958a), the tissues can be examined before their appearance alters. Ovarioles were torn apart to show follicular relics rather than the tunica dilatations.

In order to estimate the number of eggs laid, females were caught while biting, were kept for some 40 hours at a temperature of about 24°C., and then killed, or kept on ice, and dissected. By this time the developing oocytes were big enough to be counted, and the fat-body of nulliparous flies, and the follicular relics of parous flies, were often still present. When these were absent, the nulliparous or parous condition of a fly was not determined; in such cases it would be necessary to search for tunica dilatations in order to establish the egg-laying capacity of nulliparous and parous females. The developing follicles of each ovary were arranged in small flat groups in two or three rows, allowed to dry, and counted at leisure.

It was sometimes necessary to search very carefully for follicular relics because, although they are usually large and conspicuous, they shrink rapidly in flies kept for a day or more. Relics can easily be seen near the oviduct, like those of a mosquito examined by Lebed (1959), and this part of the ovary can be clearly displayed by tearing the rest of the organ in two. Some other aspects of the examination of ovarioles are included in the discussion at the end of this paper.

Certain small delicate objects, like parasitic worms and ovaries of unusual appearance, were placed in a minute drop of glycerine solution (5 parts to 95

parts, by volume, of 70 per cent. alcohol) on a cover glass. After some of the liquid had evaporated the cover glass was inverted on a cavity slide and sealed in position with Euparal.

Developing forms of *Onchocerca* or somewhat similar nematodes were recorded as being in the sausage or vermiform stages which correspond roughly to the first larval and to the second and third larval stages, respectively. Worms in the head were not described as infective because this term should also be used for some worms from the thorax if they can pass into the head while a fly is biting, as thoracic forms of *Wuchereria bancrofti* are believed by Jordan (1959) to do.

The Amani unbanded form.

Larvae and pupae.

Three species of the crab genus *Potamon* live in the Sigi and its tributaries. The common one, *P. (Potamonautes) lirrangensis* Rathbun was found at every place visited and was particularly numerous in the upper tributary. *P. (Geothelphusa) perparvum* Rathbun, a small purple species with pink claws, which was usually carrying young, was sometimes seen, particularly under stones at the edges of streams, and a small species with lateral yellow streaks was occasionally found. Apart from one young larva on the yellow-streaked crab, all the larvae and pupae were found on the common one, usually on its sides (fig. 7), although a few pupae of the unbanded form were seen in the eye sockets; in all, 336 common crabs were collected, 15 in the Mpandeni stream, in which no Simuliids were found, and 321 elsewhere; and 45 pupae, 60 pupal skins and hundreds of larvae were obtained, 37 of the pupae and 46 of the skins being of the unbanded form. Both forms were present in most collections; the unbanded one predominated in the middle and lower Sigi and the banded form in the upper Sigi and the upper tributary.

The silken holdfast (fig. 8) of the larva of the unbanded form appeared to consist of a solid pad on which were visible the impressions of many of the minute anal hooks. The holdfast of another species examined (Lewis, 1956), *S. loutetense* Grenier & Ovazza, however, was obviously a network of threads and showed no marks of teeth. When the Amani larva was removed from the glass it pulled most of the holdfast away with it, and it would be interesting to know if all these larvae on crabs grip more firmly than those on other substrata.

In view of De Meillon's suggestion (1957) (discussed later) that larvae of the *S. neavei* complex may obtain food from the crabs, the contents of the guts of some larvae of the unbanded form were examined. Like those of *S. damnosum* from the same stream, they consisted of miscellaneous débris with a few diatoms, and looked quite different from the gut contents of crabs, which were largely composed of coarse plant fragments. A larva of the unbanded form kept in a jar of hay infusion was seen to browse on the substratum, and its gut contained numerous unicellular algae.

Preserved pupae were more difficult to extract from their cocoons than were those of *S. neavei* from Uganda, probably because the loosely woven cocoons of the Amani form entangled the abdominal hooks.

The adult.

No adults were caught and nothing is known of their habits except that a female, possibly of this form, was once taken on a mule at Amani (Freeman & De Meillon, 1953; Lewis, 1960). Possibly the females, like most Simuliids (Rubtsov, 1956), can develop eggs without sucking blood.

Various observations.

Altitude.—Members of the *S. neavei* complex have usually been found at rather high altitudes, and Ovazza (1957) remarked on the relatively low altitude

of specimens which he found in West Africa about 250 metres (820 ft.) above sea level. Near Amani, members of the complex occur as low as about 500 ft., probably owing to the unusual climate mentioned above, and might conceivably occur lower still if the lower part of the river were not polluted.

A predator of the larvae.—A small fish, *Amphilius krefftii* (Siluroidea, Amphiliidae) was sometimes found among stones in the river, and the stomach contents of one, which was eight cm. long without the caudal fin, were examined; they included various insects, among them 23 Simuliid larvae of which at least eight, which were in the last instar, and probably all, belonged to the unbanded form.

The Amani banded form.

Larvae and pupae.

The early stages of this form appear to live in the same way as those of the unbanded form except for the differences in numbers in various streams.

The adult female: some structural features.

Size.—It was presumed that, as in an Anopheline (Detinova, 1944), the wing length would be a useful indication of size, and the distance from the radio-medial cross vein to the tip of the wing was measured in mm. The mean was 1.89, the median 1.88, the standard deviation 0.07, and the coefficient of variation 3.7 per cent. The results are shown in fig. 6 in comparison with measurements of

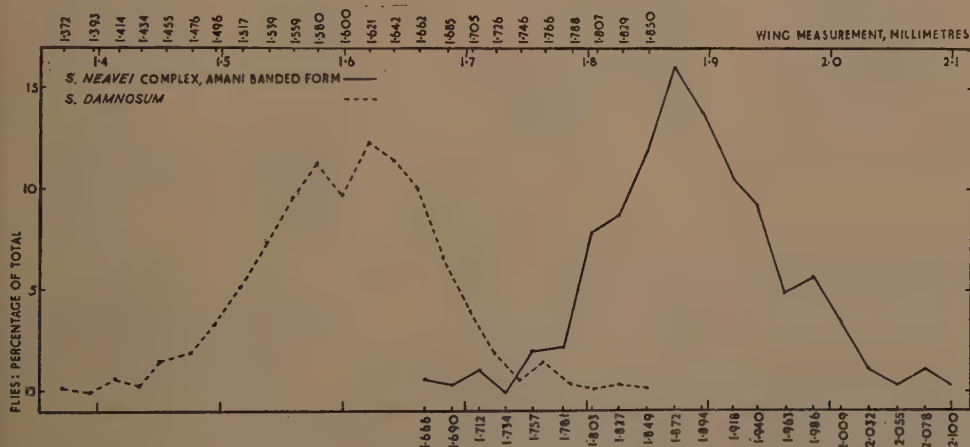
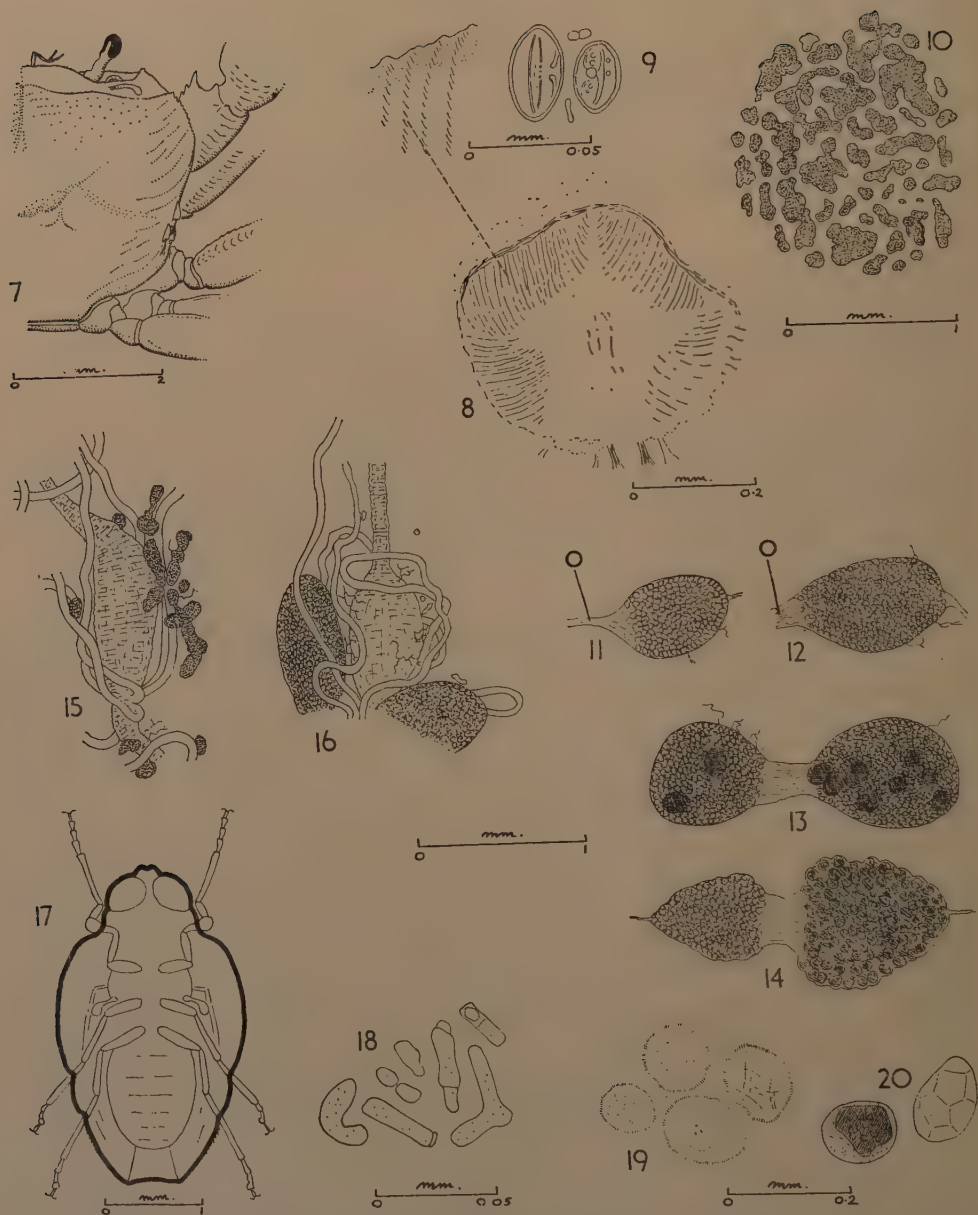


Fig. 6.—Wing measurements of females of the Amani banded form of the *S. neavei* complex compared with those of *S. damnosum* from Nigeria.

S. damnosum at Lokoja in Nigeria (calculated from widths which are roughly proportional to lengths). Although the material of *S. damnosum* probably all came from one breeding place (Lewis, 1958a) the wing size is more variable than that of the Amani banded Simuliid, possibly because the latter was studied for a shorter period.

The crop, Malpighian tubes and fat-body.—In general, the internal organs look very like those of *S. damnosum*. The crop usually contains a clear, colourless or yellow liquid, and, sometimes, pollen grains and other small objects (fig. 9). In the mid-gut of captured females a yellow meconial fluid was often seen, but



Figs. 7-20.—*S. neavei* complex. (7-8) Amani unbanded form: (7) three pupae in usual position, and two larvae near eye of crab; (8) holdfast of larva. (9-20) Amani banded form: (9) pollen grains and other objects from crop; (10) assembled sketches of central fat-body of one female; (11, 12) ovaries of nulliparous and parous females; (13) ovaries of parous female with relict eggs; (14) ovaries showing unilateral development; (15, 16) mid-gut region of nulliparous and parous females; (17) submerged female showing air bubble; (18) fungal parasites from ovary; (19, 20) ciliate parasites and unidentified objects from abdomen. o, oviduct.

no solid meconium (by contrast, in bred females of the unbanded form the meconium consisted of a single mass with little indication of its cellular origin and with a dark spot near one end). The peritrophic membrane has a narrow forward extension, as in *S. damnosum*, and is clearly visible after a blood-meal. In one female, which had fed seven hours before, it was about 7 microns thick at the side.

The Malpighian tubes of various insects change in appearance according to their condition (Detinova, 1959), and it has been found that females of *S. damnosum* with clear tubes are old and have a high *Onchocerca* infection rate. Out of 148 parous females of the banded form examined, two, taken on 24th October, had clear tubes. The ovaries of both flies were degenerated, as described later, and the head of one contained *Onchocerca* or somewhat similar nematodes. The tips of the Malpighian tubes are yellow.

The masses which comprise the central fat-body of a nulliparous fly (figs. 10, 15) have a combined volume about equal to that of the head, and those of a parous fly (fig. 16) are much reduced.

The ovaries.—In descriptions of insect ovaries the germarium end of an ovariole has been called variously the anterior, the proximal and the distal end; here it is referred to as the anterior. Alternatives for the names used for the parts of the ovary are given by Bertram (1959).

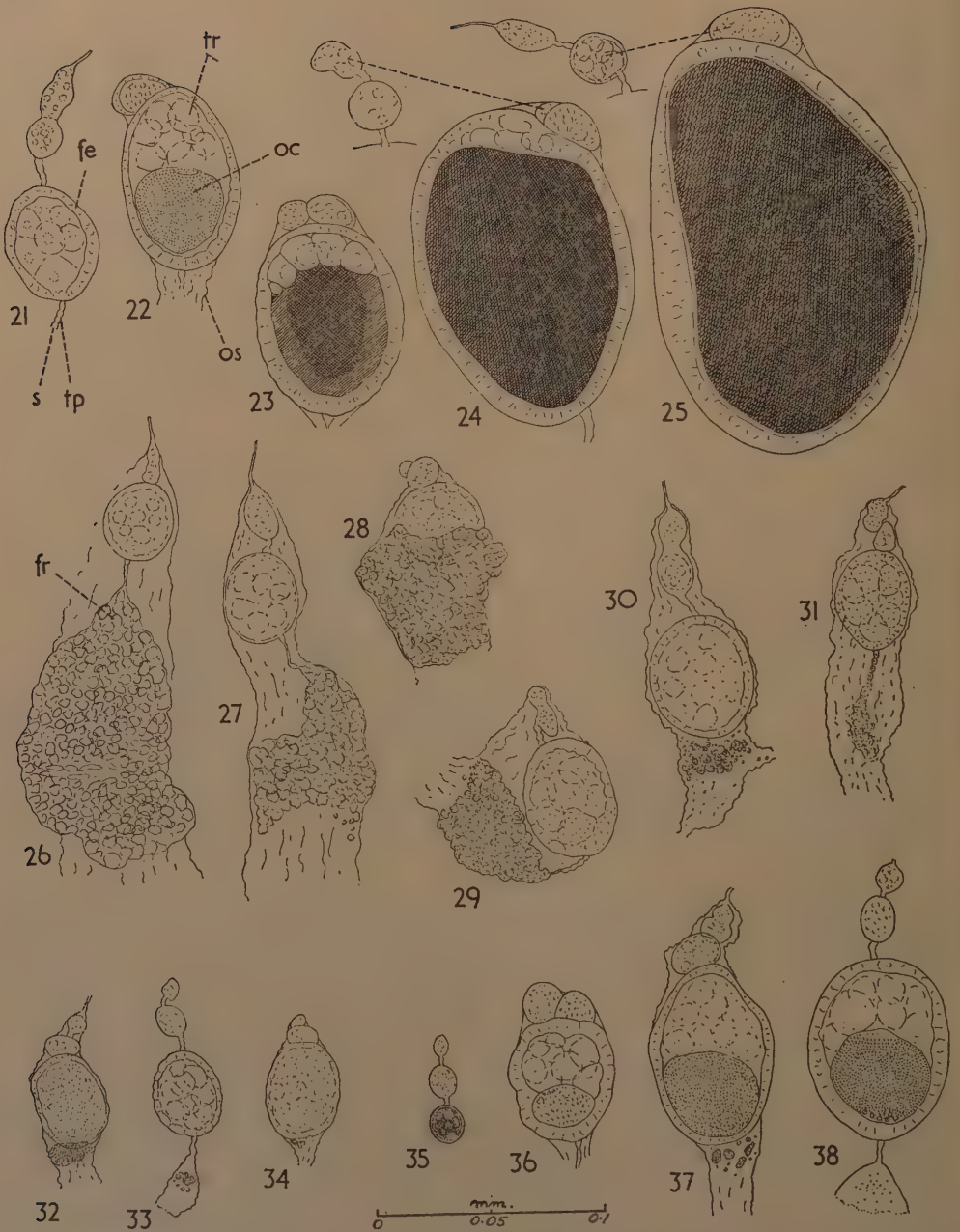
Developing eggs of seven adults were examined and found to number from 252 to 576 and to average 412. The average, however, probably has little meaning because parous flies apparently tend to lay fewer eggs than nulliparous ones.

During the first ovarian cycle (figs. 21–25), the small secondary follicles grow slightly while the primary ones are developing. If a fly, which has not recently sucked blood, is kept for two days, the appearance of the follicles may alter although they do not develop. The follicular epithelium may become very well defined, or its outline becomes irregular (fig. 32) (as in Rubtsov's fig. 11, 1958), the oocyte may grow slightly and become semi-opaque (fig. 36), and the whole follicle and its contents may become slightly yellow and cloudy (fig. 34) in contrast to the clear colourless follicles of a fresh female. Sometimes, during an ovarian cycle, a few follicles are seen to have shrunk and turned brown (fig. 35), and look very like the relics of old follicles.

A follicular relic is often about three times as large as the follicle next in succession (fig. 26) and almost colourless. It evidently consists mainly of the cells of the follicular epithelium and looks almost exactly like a partly grown follicle from which the yolk has been squeezed. In some freshly caught flies the relic is not so big (figs. 27–29), and may be about half the size of the next follicle. In flies kept for a day or two before dissection the relic may consist of only a few small granules (figs. 30–34, 37), the tunica which surrounded them being inconspicuous or invisible, although occasionally it is quite well marked (figs. 33 and 38). The smaller relics are yellow and the very small ones brown, presumably owing to the concentration of some pigment. The relics shrink rapidly even if flies are kept on ice, and it is probable that soon after being formed they become lifeless debris and shrink by a physical process, unlike living follicle cells which would retain their shape at a low temperature.

The follicular relics of the banded form were usually much larger than those of four species of *Simulium* recently examined, namely *S. neavei* in Eastern Uganda (a few), *S. damnosum* in West Africa, and *S. metallicum* Bellardi and *S. quadrivittatum* Lw. in British Honduras. The finding of large relics in the banded Simuliid, and the rapid shrinkage of relics in captive flies, together suggest that females usually bite very soon after laying eggs.

Special dissection would no doubt reveal nodes or dilatations of the tunica because up to five of these have been observed in Russian *Simulium* (Detinova, 1959; Detinova & Bel'tyukova, 1958).



Figs. 21-38.—(21-25, 35, 36) Ovariole structures of nulliparous females of the Amani banded form of the *S. neavei* complex: (21) soon after capture; (22-25) dissected 19, 21, 48 and 72 hours after blood-meals; (35) 41 hours after blood-meal; (36) 26 hours after capture, not fed on blood. (26-34, 37, 38) Ovariole structure of parous females; (26-29) soon after capture; (30-32) dissected 20, 42 and 48 hours after capture; (33) showing tunica around debris; (34) 49 hours after capture; (37, 38) dissected 45 hours after flies were captured while flies feeding. fe, follicular epithelium; fr, follicular relic; oc, oocyte; os, ovariole sheath; s, pedicel; tp, tunica; tr, trophocyte.

The ovaries of a parous fly (fig. 12) usually have a distinctive appearance. The large follicular relics retard the shrinkage of an ovary and make it semi-opaque, and the pressure within the organ forces the distal follicles and relics backwards so that they are clearly seen in the region of the oviduct. The oviduct is wrinkled and thicker than that of a nulliparous fly (fig. 11, o).

Out of 148 parous flies examined, 24 per cent. had large oocytes (fig. 13), which ranged from 1 to 11 per fly and averaged 1.2, being fewer than in *S. damnosum*. One which was measured was 0.22 mm. long.

Unilateral ovarian development was seen in some blood-fed captive flies (fig. 14).

The ovaries of lice (Kozulina, 1957) and various other insects are known to degenerate with age, and the same appears to be true of the banded Simuliid. In both the above-mentioned females with clear Malpighian tubes relict eggs were present and the ovaries showed degenerative changes. Most ovarioles were difficult to distinguish and evidently decayed, for they broke away from the calyx, which, with fragments attached to it, looked rather like an apple core. In one of these flies several follicles were partly developed, probably indicating that

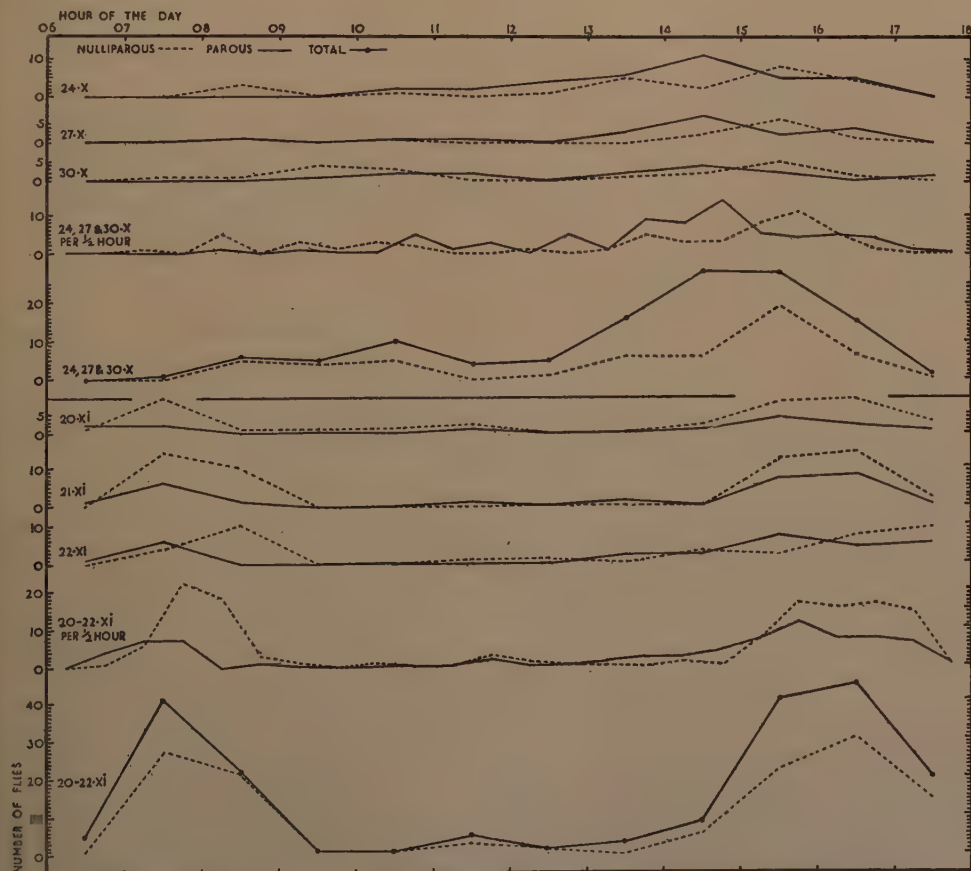


Fig. 39.—The biting times of the Amani banded form of the *S. neavei* complex during six catches.

only a fraction of the total were still active and that they had failed to mature after one blood-meal.

The biting cycle.

Mattingly (1957) has discussed the biting cycle of various Diptera, that is, the pattern of variation of biting activity at different times during the 24 hours, and has pointed out that in one or more species of *Simulium*, *Culicoides* and probably mosquitos, it is related to physiological age. Parous females of *S. damnosum* tend to bite around the middle of the day, with the result that the apparent infection rate and the risk of people being infected with *Onchocerca* depend on the time at which flies are caught or bite. Six 12-hour catches of the banded form were made at Amani to find the proportion and the actual number of nulliparous and parous flies biting at different times (fig. 39). The first series of catches was made during a ten-day period when the average shade temperature was 70.0°F., and the second at a better catching point, when the temperature averaged 74.8°. The combined results show that nulliparous and parous flies had rather different cycles and that each had one or two peaks during the day. The results for the first three days are remarkably consistent, and, like those for the second three, show that most parous flies which bite in the afternoon do so earlier than most of the nulliparous ones.

In the second series of catches there were distinct morning and afternoon peaks, respectively earlier and later than before, with a much more pronounced midday lull. This pattern and the lower proportion of parous, and of infected, flies (mentioned in the section on onchocerciasis) were probably due to the warmer weather. Evidently the best time to catch parous flies is in the early part of the afternoon peak, the exact hour depending on the season or on local conditions.

The biting cycle of parous females of the banded form and of *S. damnosum* seems to be a combination of increased activity—relative to that of nulliparous flies—in the middle hours of the day, and the general cycle of the flies as a whole which includes the midday lull. The variations in biting activity show that more investigation is required at different places and times.

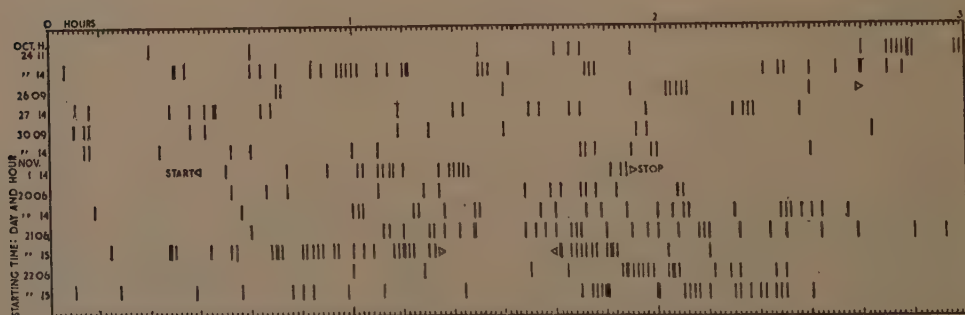


Fig. 40.—Biting times of individual flies during parts of some catches of the banded form.

Times of individual attacks.—The assistants who caught the flies recorded the time of capture of each one (fig. 40) and showed that, as in the case of *S. damnosum* and some mosquitos, people were often attacked by several flies in quick succession after a considerable interval. This is a common feature of the behaviour of some mosquitos and may be related to a resting period which occurs between the approach of a fly to its host and the actual attack. When this period is long—in *Anopheles gambiae* Giles it may be several hours (Smith, 1958)—biting times give little information about general movements.

Interval between egg-laying and biting.—As explained above, observations on the ovarioles suggest that the females bite relatively soon after laying eggs.

Other observations.

Appearance of a submerged female.—The fly shown in fig. 17 was drawn when submerged in water in a tube, to show the size of the air bubble which surrounded it.

Prevalence.—The adults were not abundant and I did not notice a single bite although I spent many hours collecting crabs in the Sigi and its tributaries. Nearly all the adults obtained were caught in two selected clearings below Amani, the better of which was rather sheltered from the wind, but even here the numbers were low. Twelve-hour catches were made in one or other of these clearings, and the daily catch, expressed as flies per man hour, ranged from 2.8 to 6.4 and averaged 4.9. People do occasionally complain of bites but the man-biting species is apparently seldom if ever numerous. Its scarcity in the forest suggests that, like *S. damnosum*, it moves more freely in the open.

Relation to onchocerciasis.

During the present work single skin smears from 30 people were examined and microfilariae, probably of *O. volvulus*, were found in 14. No symptoms have been reported.

The mild nature of the disease suggests that individual people may have light infections. If this is so it is probably due to the scarcity and localisation of the man-biting member of the *S. neavei* complex and the rather low temperature which presumably retards the development of the worm in the fly.

Barnley (1958) has suggested that *S. neavei* is a more efficient vector of onchocerciasis than is *S. damnosum*, and if this proves to be a fact it might account for the presence of the disease at Amani where the number of biting Simuliids is usually small.

Batches of nematodes from five females of the banded Simuliid were sent to Dr. G. S. Nelson who found that three of them, being only in the second stage, could only be determined as possibly *O. volvulus*, but that two, in the third stage (one being from the head), were another nematode, shorter than *O. volvulus*, lacking its characteristic hooked papillae, and having the anus much nearer the caudal extremity.

The infection rate was calculated as the percentage of the parous flies infected. This method has several advantages (Lewis, 1958a) including the saving of time, rather as Gillies (1954) did by calculating the sporozoite rate of gravid females of *A. gambiae*. Out of 359 flies dissected, 41.2 per cent. were parous, and 12.8 per cent. of these were infected with nematodes, 11.5 with thoracic, and 1.4 with head infections. In the first series of all-day catches, 55.8 per cent. of the 120 flies were parous and 14.9 per cent. of the latter were infected; in the second series (in warmer weather), of 191 flies, the figures were 33.5 and 10.9, respectively. An unusually large proportion of the nematodes found at Amani were vermiform but small.

In the mid-gut, microfilariae were seen both inside and outside the peritrophic membrane which probably traps them as does that of *S. damnosum*.

Other associated organisms.

A fungus (fig. 18) was found in the ovary of one female. In the abdomen of two others was a ciliate protozoan (fig. 19); in one instance there were about 40 individuals and the biggest was 0.16 mm. long. On several flies were grey mites, apparently all the same species, 1 to 3 in number, usually beneath the base of the abdomen. Ten were identified and proved to be *Asperoscius africanus* Chant (1957) which was described from specimens found on flowers from South

Africa. Mites of this family occur on plants where they feed on phytophagous mites. The flies probably visit flowers and pick up the mites from them. Unidentified objects (fig. 20) were found in the abdomen of one fly.

DISCUSSION.

The taxonomic status of the Amani forms.

Discussion of the taxonomic status of any members of the *S. neavei* complex must be preliminary and tentative until more is known about members of the complex in other parts of Africa, particularly *S. nyasalandicum* De Meillon and *S. woodi* De Meillon in Nyasaland. Information is required about the structure of larvae, pupae and males, and about the breeding places, commensal association and adult feeding habits. The two Amani forms are regarded as species because, although living in the same area, they differ in larval, pupal and adult structure and in adult feeding habits. The unbanded and banded forms appear to be related to *S. neavei* and *S. woodi* of Kenya, respectively, and, if the Nyasaland forms prove to differ slightly from the Kenya and Amani ones, the *S. neavei* complex may be found to consist largely of various subspecies of these two species.

The Amani forms differ biologically from the above-mentioned Kenya species. The unbanded form, unlike *S. neavei*, has not been found biting man. The banded form, unlike the *S. woodi* of Kenya, pupates externally on the crab and bites man readily. The relation of the larvae of the two Amani forms to crabs and the extent to which they are necessarily associated with woodland can not be fully compared with that of the Kenya species because at Amani there is only one common crab, which, unlike the common Kenya crabs, is not restricted to either open or shaded water, and because the Sigi is unsuitable for Simuliids after it leaves the forest area.

The study of ovarioles.

In recent years much attention has been paid to the ovarioles of mosquitos and some other Diptera because their condition can provide information about physiological age. Detinova (1959) and W. N. Beklemishev, T. S. Detinova & V. P. Polovodova (*Bull. World Hlth Org., in press*) have given extensive accounts of work by themselves and others on various Diptera, and Bertram (1959), Gillies (1958b) and Lewis (1958b) have discussed the ovarioles of certain mosquitos.

In addition to studying the ovaries of the banded Simuliid at Amani, I have briefly examined those of species of TIPULIDAE, CERATOPOGONIDAE (Lewis, 1959), PSYCHODIDAE, SIMULIIDAE, CULICIDAE, TABANIDAE (Lewis, *in press*), STRATIOMYIDAE, MUSCIDAE and CALLIPHORIDAE.

Some aspects of stages in ovariole development of various Diptera are discussed below in view of their relevance to the appearance, during dissection, of the latest follicular relic in the Amani banded form of the *S. neavei* complex.

Some structures in an ovariole before ovulation.

Structures which are of interest in relation to the appearance which an ovariole will have after ovulation are the nurse cells, or trophocytes (perhaps sometimes to a negligible extent), the follicular epithelium, the terminal stalk or pedicel, connecting stalks and the part of the tunica which covers the epithelium and stalks. All these structures are surrounded by the ovariole sheath which corresponds to the outer epithelial sheath of the polytrophic ovariole of an earwig, which is figured by Bonhag (1958).

In some Diptera at least, the cells of the follicular epithelium evidently shrink during the growth of an oocyte. Nath (1924) found that those of *Culex* lose

their individuality, contribute to the formation of the chorion, and ultimately disappear.

The pedicel corresponds in position, and probably in fact, to the typical insect pedicel which consists of a tube of epithelium and is blocked anteriorly by a plug. A pedicel in *Simulium*, *A. gambiae*, *Mansonia fuscopennata* (Theo.) and various other mosquitos appears to consist of a single row of cells, but that of *Phlebotomus papatasi* (Scop.) has been found by B. Jobling (personal communication) to contain many cells and may perhaps form a cellular tube at the time of ovulation. Nicholson (1921) found that in *A. maculipennis* Mg. (*sensu lato*) the pedicel runs back to join the wall of the calyx, and Giglioli (1959) has described this junction in *A. gambiae*.

A connecting stalk is very like the pedicel but shorter, at least in *A. maculipennis* according to Detinova (1959), Nicholson (1921) described the development of a connecting stalk, on one side of the ovariole axis, from the septum which separates the germarium from a young follicle and gives rise to part of the epithelium of the latter.

The part of the tunica covering the stalks has a segmented appearance corresponding to the outline of the cells beneath, and forms a series of tubes which are much narrower than those in some insects with thick pedicels and interfollicular tissue. These narrow tubes later contribute to the rosary-like formation of the tunica in an old fly after ovulation.

Ovulation.

It would be difficult to follow the process of ovulation—the passage of an egg into the calyx—which may be quite rapid. Dissection would interfere with the natural process, and sections, even if they could be suitably timed, might be difficult to interpret because the ovarian structures are closely packed together.

The fate of the follicular epithelium is of special interest. According to Wigglesworth (1949) the egg, in some mosquitos, is ovulated by the rupture of the follicle, and it would appear that this often occurs while the egg is still inside its section of the tunica—to judge from the amount of epithelium seen in the tunica dilatations or nodes of some mosquitos and Simuliids. Nicholson (1921) found that the ovariole sheath of *A. maculipennis* contracts forward, leaving the fully formed egg lying in the calyx and still surrounded by the follicular epithelium—now degenerated into a mere membrane—and that the egg apparently bursts through this before being laid. During ovulation in this insect most or all of the follicular epithelium evidently breaks away from its suspensory stalk without releasing the egg which it surrounds.

The period between ovulation and dissection.

In general the cells of the follicular relic of an insect degenerate, undergo autolysis and ultimately disappear (Wigglesworth, 1953). Schlottman & Bonhag (1956) have studied the degenerative process in *Tenebrio molitor* L., in which the cell walls disappear, the nuclei dissolve, the cells continue to degenerate until the relic has almost completely deteriorated, and finally are apparently absorbed or discharged. Singh (quoted by Lewis, 1958b) found that in *Locusta migratoria migratorioides* (R. & F.) the cells last long enough for three relics to be seen at the same time.

The relics in the Amani banded Simuliid shrink rapidly and it remains to be seen if they disappear altogether in a blood-starved parous fly.

The appearance of a follicular relic at dissection.

The size of the follicular relic seen in a dilatation of the tunica evidently depends on four factors—three of which have been considered above—the original composition of the epithelium, the amount of shrinkage which it undergoes when

the oocyte is developing, the quantity of epithelium—if any—which emerges from the dilatation at ovulation, and the time which elapses between ovulation and dissection.

Follicular relics naturally vary greatly in appearance in various Diptera, and it seems that two main types are to be seen shortly after ovulation. In one type many cells form the relic and look rather like peas in a bag, the bag being the tunica dilatation which is difficult to distinguish from the outline of the cells. Examples are the Amani banded *Simulium*, and *Chrysops bicolor* Cordier (Lewis, *in press*) and others could be quoted. In the other type the relic is so small that the dilatation, not yet fully contracted—looks like a rather empty sac. Examples are *A. maculipennis* (Detinova, 1959) and *Phlebotomus papatasi* (Dolmatova, 1942).

Possible sources of error in the examination of follicular relics and tunica dilatations.

It is advisable at this point to draw attention to various pitfalls which await an inexperienced observer of Simuliids and some other Diptera. He may either fail to find relics or dilatations when they are present, or mistake other objects for them, particularly in small biting insects.

Relics can escape notice for various reasons. They may be very small or disappear during dissection, or be hidden by follicles, burst yolk or other objects; and in preparations which are stained or viewed with artificial light the distinctive colour of small relics is lost.

One of the objects which may be mistaken for a dilatation of the tunica is a piece of torn ovariole sheath attached to the posterior end of a follicle. The piece of sheath, however, unlike a dilatation, is broadly attached to the follicle. A piece of tracheole attached to the end of a stalk can look like a fragment of a dilatation. The 'segments' of a stalk can be mistaken for a series of dilatations. If a dilatation of *C. bicolor* is compressed during dissection a constricted part of it can be mistaken for one of the stalks, which are not 'segmented' in this species. When a nulliparous pre-gravid female of *Chrysops* or *Simulium* is examined in order to count the developing follicles a degenerate yellow follicle may be mistaken for an old relic. The former can be recognised by its position (the follicle anterior to it corresponding to those anterior to developing ones) and by its degenerating epithelium. Sometimes a growing oocyte is accidentally squeezed out of its follicle which then becomes a relic and looks like a normal one.

The association between Simuliids and crabs.

This discussion is not concerned with the special case of larvae and pupae of *S. woodi* in Kenya and Uganda—considered by Grenier & Mouchet (1958)—which live in the anterior openings of the branchial chamber of a crab (McMahon, 1957; Barnley & Prentice, 1958) and should perhaps be regarded as parasites.

Terminology.

The association between Simuliid larvae and crabs has often been called phoresy. The derivation of this word implies "the carriage of one organism by another, without parasitism," to quote the definition of "phoresia" by Henderson & Henderson (1949). Hesse & Doflein (1943), however, use the term for the temporary attachment of an organism to another capable of more rapid locomotion, and liken the former to a stowaway and the latter to an aeroplane or a horse. Clay & Meinertzhagen (1943) employ "phoresy" to describe the carriage of lice by birds, and Allee & others (1949) refer to it as a form of commensalism in which the guest is transported by the host and receives no other benefit, and they give examples of the resulting dispersal. Allee & Schmidt (1951) use "phoresy" to describe the "dispersal of small non-parasitic terrestrial animals

by temporary attachment to flying forms," and Baer (1951) and others emphasise travel as an essential feature of the phenomenon. We do not know what advantage the Simuliids gain, and it seems unlikely to be extensive transport which has not even been suggested. It is therefore appropriate to reject the term phoresy, as do Grenier & Mouchet (1958) for other reasons, and to refer to the relationship simply as an association or possibly as commensalism.

Allee & others (1949) describe commensalism as an ecological union in which both parties do not benefit but neither is harmed, and they point out that, as in the case of naiads on aquatic insects, when the supporting animal is active the passive guest may obviously benefit by avoiding stagnant water.

Possible advantages to the larvae and pupae.

De Meillon (1957), on the basis of Marlier's observations on *Simulium* larvae on may-fly nymphs, has suggested that larvae of the *S. neavei* complex obtain food from the crabs, but the few observations on gut-contents at Amani do not support this hypothesis. The findings of a larva-eating fish at Amani shows that any protection afforded by the crabs may be very limited. Most of the larvae, being near the inhalent openings of the crab, may benefit from its respiratory current when the animal is in a pool. None of these possible advantages, however, seem likely to be the main result of the association.

The larvae of *Simulium*, unable to swim, have limited powers of movement, particularly upstream, and the pupae are sessile. Each species is suited to a certain range of current, and changes in water-level or larval drift can place it in an unsuitable environment. The larvae and pupae of the *S. neavei* complex, however, are on a living platform which can carry them to a suitable current beneath stones and thus save them from natural hazards. The crabs are already known to protect them from the artificial danger of strong insecticide (McMahon, Highton & Goiny, 1958). The importance of water current in the association between Simuliids and the animals (Ephemeroptera and crabs) which carry them is evident from the interesting discussions on the subject by Grenier & Mouchet (1958) and by Rubtsov whom they quote.

If the crabs do help the Simuliids to avoid these immediate dangers they probably also confer a long-term benefit. McMahon (personal communication) reported that, when he knew the breeding places of *S. neavei* but had not yet discovered its pupae, he expected that they would have short robust gills like those of other species living in fast streams. The slender delicate gills of the *S. neavei* complex are to be expected on pupae inhabiting small, usually slow, streams like the Amani upper tributary but seem out of place in the turbulent Sigi where they contrast with those of *S. debegeni* and *S. damnosum*. The structure of the gills in the *S. neavei* complex suggests that these species are derived from a form which bred in small streams, and that, by associating themselves with crabs, they have been able to breed in both slow and fast streams and thus extend their range.

The crab association may have some disadvantages for the Simuliids. Each larva presumably has to find a crab, and when it is attached it may be carried into nearly still water.

Various other animals live on the bodies of Crustacea. Some of those which occur on marine crabs are thought to get food from their hosts (Yonge, 1949). An American Corixid bug, which lives in stagnant water, lays its eggs on a crayfish (Abbott, 1912; Hungerford, 1919, 1948) whose respiratory movements create a current. On the coast of East Africa a mosquito lays its eggs on a swamp crab (Goiny, van Someren & Heisch, 1957) which may perhaps keep them near the water surface. Near Kumba in the Cameroons I have recently found Chironomid larvae on many fresh-water crabs; the larvae occur singly in tunnels on the side of the body above the legs.

Summary.

The paper deals with two members of the *Simulium neavi* Roub. complex found at Amani in the forest of the Usambara Mountains, Tanganyika Territory. They have already been described but are at present termed the Amani unbanded and banded forms, scientific names being withheld until the taxonomy of the whole complex is better understood.

Some methods of study are described.

Pupae of the unbanded form constituted a large proportion of the total number found on the common local crab, *Potamon* (*Potamonautes*) *lirrangensis* Rathbun, which amounted to roughly one pupa to seven crabs. This form predominated in the lower and more open parts of the drainage system examined. The adults were not seen to bite man. This and the banded form were found at a much lower altitude than any hitherto reported for the complex, probably owing to the particular nature of the local climate. Neither form was abundant.

The larvae and pupae of the banded form, like the unbanded one, live externally on the crabs. The variability of wing size of the banded form is described. Observations were made on the internal anatomy of the adult with special reference to the ovaries in which the follicular relics are usually very large, indicating that the female probably bites soon after laying eggs. As in *S. damnosum* Theo. there is an easily recognisable class of old flies with clear Malpighian tubes. Nulliparous and parous flies have rather different biting cycles. The banded form bit man readily but only about five were taken per hour in good catching places and far fewer elsewhere.

Human onchocerciasis has been reported from Amani but is not known to do any harm there. The existence of the disease in the presence of rather small numbers of Simuliids is of interest in relation to a belief that *S. neavei* is a more efficient vector of onchocerciasis than is *S. damnosum*. Out of 359 banded females dissected 41.2 per cent. were parous and 12.8 per cent. of these were infected with nematodes, at least some of which were not *Onchocerca volvulus*.

Taxonomy, the ovarioles and the Simuliid-crab association are discussed. The formation of the large follicular relics of the banded form is considered in relation to the history of the follicular epithelium before and after ovulation. The crab association is regarded as commensalism, and it is suggested that the crabs benefit the Simuliids by carrying them a short distance to a suitable current and that they thus enable them to live in fast rivers and so extend their range.

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References.

- ABBOTT, J. F. (1912). An unusual symbiotic relation between a water bug and a crayfish.—*Amer. Nat.* **46** pp. 553–556.
- ALLEE, W. C., EMERSON, A. E., PARK, O., PARK, T. & SCHMIDT, K. P. (1949). Principles of animal ecology.—837 pp. Philadelphia, Pa., Saunders.
- ALLEE, W. C. & SCHMIDT, K. P. (1951). Ecological animal geography.—2nd edn., 715 pp. New York, Wiley.
- BAER, J. G. (1951). Ecology of animal parasites.—224 pp. Urbana, Ill., Univ. Ill. Pr.
- BARNLEY, G. R. (1958). Control of *Simulium* vectors of onchocerciasis in Uganda.—*Proc. 10th int. Congr. Ent.* **3** 535–537.
- BARNLEY, G. R. & PRENTICE, M. A. (1958). *Simulium neavei* in Uganda.—*E. Afr. med. J.* **35** pp. 475–485.
- BERTRAM, D. S. (1959). The ovary and ovarioles of mosquitos.—W.H.O./Mal./238 pp. 170–186, multigraph.
- BONHAG, P. F. (1958). Ovarian structure and vitellogenesis in insects.—*Annu. Rev. Ent.* **3** pp. 137–160.
- CHANT, D. A. (1957). Descriptions of two new Phytoseiid genera (Acarina: Phytoseiidae), with a note on *Phytoseius* Ribaga, 1902.—*Canad. Ent.* **89** pp. 357–363.
- CLAY, T. & MEINERTZHAGEN, R. (1943). The relationship between Mallophaga and Hippoboscid flies.—*Parasitology* **35** pp. 11–16.
- DE MEILLON, B. (1957). Bionomics of the vectors of onchocerciasis in the Ethiopian geographical region.—*Bull. World Hlth Org.* **16** pp. 509–522.
- DETINOVA, T. S. (1944). The relationship between the size of female *Anopheles maculipennis atroparvus* Thiel and the stage of development of the ovaries on emergence.—*Med. Parasit.* **13** pp. 52–55.
- DETINOVA, T. S. (1959). Course in advanced entomological techniques applied to malaria eradication.—W.H.O./Mal./238 pp. 5–169, multigraph.
- DETINOVA, T. S. & BEL'TYUKOVA, K. N. (1958). On the number of gonotrophic cycles in black flies (Simuliidae) near Krasnoyarsk (Siberia). [*In Russian with English summary.*]—*Med. Parasit.* **27** pp. 686–688.
- DOLMATOVA, A. V. (1942). The life-cycle of *Phlebotomus papatasi* (Scopoli). [*In Russian.*]—*Med. Parasit.* **11** no. 3 pp. 52–70.
- FREEMAN, P. (1957). The problem of the *Simulium neavei* complex.—*Bull. World Hlth Org.* **16** pp. 669–670.
- FREEMAN, P. & DE MEILLON, B. (1953). Simuliidae of the Ethiopian region.—224 pp. London, Brit. Mus. (Nat. Hist.).
- GABATHULER, M. J. & GABATHULER, A. W. (1947). Report of onchocerciasis in the Ulanga District (Eastern Province, T.T.).—*E. Afr. med. J.* **24** pp. 188–195.
- GIGLIOLI, M. E. C. (1959). Observations on the structure of the ovariole and the follicular residue body or corpus luteum in *Anopheles gambiae*.—*Trans. R. Soc. trop. Med. Hyg.* **53** pp. 310–311.
- GILLIES, M. T. (1954). The recognition of age-groups within populations of *Anopheles gambiae* by the pre-gravid rate and the sporozoite rate.—*Ann. trop. Med. Parasit.* **48** pp. 58–74.
- GILLIES, M. T. (1958a). A modified technique for the age-grading of populations of *Anopheles gambiae*.—*Ann. trop. Med. Parasit.* **52** pp. 261–273.

- GILLIES, M. T. (1958b). A review of some recent Russian publications on the technique of age determination in *Anopheles*.—*Trop. Dis. Bull.* **55** pp. 713–721.
- GOINY, H., VAN SOMEREN, E. C. C. & HEISCH, R. B. (1957). The eggs of *Aedes* (*Skusea*) *pembaensis* Theobald discovered on crabs.—*E. Afr. med. J.* **34** pp. 1–2.
- GRENIER, P. & MOUCHET, J. (1958). Premières captures, au Cameroun, d'une *Simulie* du complexe *neavei* sur des crabes de rivières et de *Simulium berneri* Freeman sur des larves d'Ephémères. Remarques sur la signification biologique de ces associations.—*Bull. Soc. Path. exot.* **51** pp. 968–980.
- HENDERSON, I. F. & HENDERSON, W. D. (1949). A dictionary of scientific terms.—4th edn. Edinburgh, Oliver & Boyd.
- HESSE, R. & DOFLEIN, F. (1943). Das Tier als Glied des Naturganzen.—*Tierbau u. Tierleben* **2**, 828 pp. Jena, Fischer.
- HUNGERFORD, H. B. (1919). The biology and ecology of aquatic and semiaquatic Hemiptera.—*Kans. Univ. Sci. Bull.* **11** pp. 3–265.
- HUNGERFORD, H. B. (1948). The Corixidae of the Western Hemisphere.—*Kans. Univ. Sci. Bull.* **32** pp. 1–827.
- JORDAN, P. (1956). Filariasis in the Eastern, Tanga and Northern Provinces of Tanganyika.—*E. Afr. med. J.* **33** pp. 225–233.
- JORDAN, P. (1959). A note on the effect of a blood meal on infective larvae of *Wuchereria bancrofti* in *Culex fatigans*.—*Trans. R. Soc. trop. Med. Hyg.* **53** pp. 148–150.
- KEMP, J. F. (1957). The Leon tube: an instrument for measuring flow speeds in water.—*J. sci. Instrum.* **34** pp. 390–392.
- KOZULINA, O. V. (1957). On the morphology and biology of *Pediculus humanus corporis* De Geer (Anoplura, Pediculidae). [In Russian with English summary].—*Rev. Ent. URSS* **36** pp. 577–597.
- LEBIED, B. (1959). Détermination de l'âge physiologique des Diptères . . .—*Riv. Parassit.* **20** pp. 91–106.
- LEWIS, D. J. (1956). The medical entomology of the Tonkolili Valley, Sierra Leone.—*Ann. trop. Med. Parasit.* **50** pp. 299–313.
- LEWIS, D. J. (1958a). Observations on *Simulium damnosum* Theobald at Lokoja in Northern Nigeria.—*Ann. trop. Med. Parasit.* **52** pp. 216–231.
- LEWIS, D. J. (1958b). The recognition of nulliparous and parous *Anopheles gambiae* by examining the ovarioles.—*Trans. R. Soc. trop. Med. Hyg.* **52** pp. 456–461.
- LEWIS, D. J. (1959). Some observations on Ceratopogonidae and Simuliidae (Diptera) in Jamaica.—*Ann. Mag. nat. Hist.* (13) **1**, pp. 721–732.
- LEWIS, D. J. (1960). The *Simulium neavei* complex (Diptera, Simuliidae) at Amani in Tanganyika.—*Proc. R. ent. Soc. Lond.* (B) **29**.
- LEWIS, D. J. (in press). Notes on *Chrysops bicolor* Cordier in Tanganyika.—*Proc. R. ent. Soc. Lond.* (A) **35**.
- McMAHON, J. P. (1957). Notes on the *Simulium neavei* group of Simuliidae with particular reference to *S. nyasalandicum* and *S. woodi*.—*Bull. ent. Res.* **48** pp. 607–617.
- McMAHON, J. P., HIGHTON, R. B. & GOINY, H. (1958). The eradication of *Simulium neavei* from Kenya.—*Bull. World Hlth Org.* **19** pp. 75–107.

- MATTINGLY, P. F. (1957). Genetical aspects of the *Aedes aegypti* problem. I. Taxonomy and bionomics.—*Ann. trop. Med. Parasit.* **51** pp. 392–408.
- MOREAU, R. E. (1933). Pleistocene climatic changes and the distribution of life in East Africa.—*J. Ecol.* **21** pp. 415–435.
- MOREAU, R. E. (1935). A synecological study of Usambara, Tanganyika Territory, with particular reference to birds.—*J. Ecol.* **23** pp. 1–43.
- NATH, V. (1924). Egg-follicle of *Culex*.—*Quart. J. micr. Sci.* **69** pp. 152–175.
- NICHOLSON, A. J. (1921). The development of the ovary and ovarian egg of a mosquito, *Anopheles maculipennis*, Meig.—*Quart. J. micr. Sci.* **65** pp. 395–448.
- OVAZZA, M. (1957). Présence de Simulies du “ groupe *neavei* ” au Moyen Congo, Afrique Equatoriale Française.—*Bull. Soc. Path. exot.* **50** pp. 537–539.
- RUBTSOV, I. A. (1956). Nutrition and facultativity of bloodthirstiness in black-flies. [In Russian with English summary.]—*Rev. Ent. URSS* **35** pp. 731–751.
- RUBTSOV, I. A. (1958). The gonotrophic cycle in blood-sucking black flies (Simuliidae). [In Russian with English summary.]—*Parazit. Sborn. Zool. Inst. Akad. Nauk SSSR* **18** pp. 255–282.
- SCHLOTTMAN, L. L. & BONHAG, P. F. (1956). Histology of the ovary of the adult mealworm *Tenebrio molitor* L. (Coleoptera, Tenebrionidae).—*Univ. Calif. Publ. Ent.* **11** pp. 351–394.
- SMITH, A. (1958). Outdoor cattle feeding and resting of *A. gambiae* Giles and *A. pharoensis* Theo. in the Pare-Taveta area of East Africa.—*E. Afr. med. J.* **35** pp. 559–567.
- WELCH, P. S. (1948). Limnological methods.—Philadelphia, Pa., Blakiston.
- WIGGLESWORTH, V. B. (1949). The physiology of mosquitoes. In Boyd, M. F. *Ed. Malariaology* **1** pp. 284–301. Philadelphia, Pa., Saunders.
- WIGGLESWORTH, V. B. (1953). The principles of insect physiology.—5th edn., 546 pp. London, Methuen; New York, Dutton.
- WOODMAN, H. M. (1958). Filariasis with special reference to *Loa Loa* and *Onchocerca volvulus*.—*E. Afr. med. J.* **35** pp. 457–465.
- YONGE, C. M. (1949). The sea shore.—311 pp. London, Collins.

THE LIFE-HISTORY OF THE MELON WEEVIL, *BARIS GRANULIPENNIS* (TOURN.), IN ISRAEL.

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(PLATE V.)

The melon weevil, *Baris granulipennis* (Tourn.), once hardly known to agriculturists and local entomologists, has now become a serious pest in Israel. It causes considerable damage to cucurbit crops particularly in the southern part of the country.

That the insect was also of little economic importance in Egypt, where it was first described, may be inferred from records in the literature. The species was first described in 1874 and has been mentioned only twice as a crop pest; it was recorded in Egypt as emerging from water-melon fruits in large numbers (Adair, 1917) and previously had been found attacking *Colocynthis vulgaris*.

In Israel the writer made a search in most of the local entomological insect collections, the earliest of which date back to the early nineteen-twenties. In none of these, except that of the Agricultural Research Station, were there specimens dated earlier than 1938 although as far as the writer is aware insect collectors were quite active during the 15 years prior to this date.

The earliest record in the above-mentioned collection is of specimens found on the wild *Colocynthis* sp. in November 1934 by H. Z. Avidov. The second record is that by the present writer who bred many weevils from young water-melon fruits in June 1935. The question which arises is: Was this species recently introduced from Egypt or has the weevil always existed in Israel but remained rare until conditions were favourable enough to permit increase? It is difficult to decide. Some farmers claim to have seen in the remote past worms in water-melons, but no one can tell which worm. On the other hand, some farmers in the northern part of the country and in the Jordan Valley claim to have never seen this pest before. Bodenheimer does not mention this species in his works of 1930, 1935 and 1937.

In view of the fact that so little was known about this pest, a study was undertaken which is presented below.

Hosts.

So far, the weevil has been found in fruits of water-melon (*Colocynthis citrullus*), both wild and cultivated, other melons of all varieties, and cucumbers. It has never been found in vegetable marrow or squashes. Usually young, soft fruit is attacked, from the size of a walnut, or even smaller, to the size of a grapefruit.

Damage.

The adults feed on leaves, stems and young fruit of the above-mentioned hosts. However, this feeding causes no loss; it is the act of oviposition which damages the fruit. Prior to oviposition the female gnaws a girdle around the stem end of the fruit, so that its growth is stunted. Then she gnaws several holes in the peel (Pl. V, fig. 1) and one egg is laid in each. Weevils usually appear when the first fruits of the season begin to develop. This prevents the farmer from marketing early fruit when prices are more favourable.

Furthermore, as pointed out below, it may happen that the fruit stem is not girdled, and the fruit continues to grow harbouring live larvae. Infested ripe fruit may thus reach the market. Such infestation is a matter for serious concern where the fruit is grown for export, since interception of larvae at the port of entry may discredit the exporters and so lead to a loss far greater than the value of the damaged fruit.

Distribution.

To date the pest has been recorded in Egypt and Israel. It would seem likely that it may prove to occur also in Jordan and in some North African countries.

Biology.

The insect emerges from its winter quarters towards the end of May. Infested fruits are found early in June, many containing more than 100 holes, probably the result of oviposition by several females. Many of these holes are simply cavities which contain no eggs. A single fruit, however, may contain more than 5-6 dozen larvae.

The egg.

The egg-cavity has a narrow opening which broadens into a tunnel leading sideways to a depth of about 2 mm. This form of cavity is due to the curvature of the rostrum. The egg is ellipsoidal, whitish and translucent, about 0.6 mm. long and 0.3 mm. wide. As it develops its dimensions increase.

The incubation period was studied either by opening oviposition cavities at fixed periods after removal of the females from the fruit, or by removing eggs and placing them on moist blotting paper in a petri dish.

The incubation period at three temperatures is shown in Table I. The figures were averaged from eggs laid by first- and second-generation females as no difference was observed in their physiology.

TABLE I.

Incubation period of eggs of *Baris granulipennis*.

No. of cultures	No. of eggs	Temperature (°C.)	Mean incubation period (days)	No. of eggs surviving	% survival
8	160	22	6 (4-7)	104	65
8	162	26	3.9 (3-11)	114	70
10	129	30	3.7 (3-5)	79	61

The larva.

Upon hatching, the larva burrows into the pulp, searching for seeds on which to feed. Should the seed coat itself be too hard for ingestion, the larva gnaws through it and empties the contents of the shell. To study the length of larval development, young water-melon fruits were put into a jar with several laying females. A day or two afterwards they were removed. At various periods fruits were opened to study conditions inside.

In 1958, over 90 such cultures were established, but only few records (Table II) were obtained for the following reasons: (1) fruits very often decayed before the larvae reached pupation; conditions improved but little when the fruits were placed

outdoors in the sun; (2) many fruits became contaminated with larvae of *Atherigona excisa* (Thoms.). The flies oviposited in the holes made by the weevils and the maggots devoured the *Baris* larvae: that this was the case was proved when maggots were isolated and placed with *Baris* larvae in a petri dish. The three records of 1953 were from infested fruits brought from the field with signs of recent oviposition.

As the table shows, there is great variation in the length of development even at the same temperature. It was noticed that larvae when mature did not pupate if the surroundings were too moist: they continued to wander until favourable dry conditions were found, otherwise they died, presumably on account of excess moisture. Since the fruits used in the various cultures were of different sizes, *i.e.*, with varying ratios of pulp to water, the length of period from egg to pupation also varied.

TABLE II.

Length of development of *Baris granulipennis*.

Date of oviposition	Beginning of pupation	Egg and larval period (days)	Emergence of adults	Shortest pupal period (days)	Total development (days)	Average temperature (°C.)
29-31.v.53	21.vi	18-20	—	—	—	25
3-5.vi.53	28.vi	23-25	9.vii	11	34-36	26.4
25-27.vii.53	—	—	5.ix	—	41	27.8
21-22.vii.58	8.viii	17-18	—	—	—	27.5
21-22.vii.58	14.viii	23-24	—	—	—	28.5
27-29.vii.58	12.viii	15-17	26.viii	14	29-30	28
29-31.vii.58	16.viii	16-18	—	—	—	27.5
1-3.viii.58	15.viii	12-14	26.viii	11	25	28
21-22.viii.58	—	—	23.ix	—	32-33	24.5
22-24.viii.58	20.ix	27-29	—	—	—	27
24-25.viii.58	—	—	3.x	—	39-40	24.5
29-31.viii.58	—	—	2.x	—	32-34	24.5
31.viii.58	21.ix	21	7.x	16	37	26
5-7.ix.58	—	—	8.x	—	31-33	25.4
1-4.ix.58	26.ix	22-25	8.x	12	34-37	25

Pupation.

In fruits the size of a tennis ball, or even smaller, the feeding of numerous larvae converts the pulp into a spongy mess (Pl. V, fig. 2), which later dries and ultimately dwindles down to a spoonful of refuse. Such debris affords an optimal site for pupation. Meanwhile the peel of the fruit hardens into a shell perforated with oviposition holes.

When such a dried and shrunken fruit is opened one may find the dark- or light-brown cocoons arranged very much like sealed honey-comb cells (Pl. V, fig. 3). Microscopic and chemical examinations showed them to consist of brittle organic matter containing about 20 per cent. albumin.

Formation of cocoon.—Mature larvae, about to pupate, were placed in a petri dish together with a little fruit refuse. They soon covered themselves with this material and began to build the cocoon. The process could be observed with the aid of a low-power binocular microscope when the glass dish was turned over.

To obtain material for the cocoon the larva bends so that the head reaches the end of the abdomen. The mandibles grasp the tip of the abdomen squeezing it a few times with a 'milking' action. Then the larva takes a bit of the surrounding refuse into the mouth, mixing it with the viscid fluid squeezed from

the anus and forms a minute pellet. This process is repeated again and again. The pellets, dried and hardened, serve as the cocoon building material. They are glued to each other and placed first over the ventral part of the body so that a minute disc is formed in its middle. New pellets are glued laterally in both directions, thus forming a half girdle whose lateral ends are glued to the substratum. The larva proceeds next to glue new pellets to the anterior margin until the thorax is hidden. Without completing this end it turns around and adds new pellets to the posterior margin until that end of the cell is closed. Then it turns around again and closes the anterior part of the cell. The building of such a cocoon may take a day.

For comparison, cocoon-making of other CURCULIONIDAE was observed, namely, in a few species of *Hypera*. In these too the viscid material is squeezed from the anus, but the pure material alone is used in the spinning of the cocoon. The droplet is fastened to the plant or to a previously fastened hardened thread and is drawn out into rough, tapering irregular threads. Dissection of larvae showed that the Malpighian tubules of mature larvae to be greatly enlarged and to fill the entire body cavity. It seems likely that in both *Baris* and *Hypera* the viscid fluid is derived from the Malpighian tubules.

Factors preventing cocoon-making.—As mentioned, an environment too watery prevents pupation. When a larva is removed from a dried fruit into a fresh one, it will not build the cell although it is physiologically mature.

Occasionally a fruit in which eggs had been laid was not girdled and its growth not stunted (this happens if the laying female girdles the leaf stalk rather than the fruit stalk). Then larvae develop simultaneously with the growing fruit. Live larvae or traces of feeding may be found in such fruit, which are bitter to the taste, or tainted, but pupal cells were never found.

Oviposition.

In order to study the preoviposition period, the laying of eggs and their number, several pairs of adults were isolated a day or two after their emergence from the pupal cocoon. Each pair was placed in a 2-cm. section of a plastic tube 2 cm. in diameter. This tube was affixed to a young water-melon fruit, one end opening on the fruit and the other closed with cheese cloth. Six to ten such cells could be placed upon a single fruit, thereby economising in fruits when they were not too plentiful. All fruits were changed every other day and the number of eggs from each female was recorded.

In addition to breeding from individual pairs, several pairs were placed together in a jar with a fruit to oviposit. In each case water-melon leaves were supplied as food. A culture was established of nine pairs selected from weevils of the second generation. The preoviposition period at room temperature, which averaged about 27–28°C., was four days. Mating was observed on the second day after emergence from the pupal cocoon. Some of the females continued to lay from the middle of August to about the end of October. As shown in fig. 1, the peak of oviposition was about two weeks after emergence. The number of eggs per female ranged from 10–71, the average being 40.

A different picture was obtained when the nine pairs of weevils from the same lot were placed together. The preoviposition period was the same and the climax of oviposition was also reached two weeks after emergence. The rate of oviposition, however, was somewhat different; the number of eggs laid was 674, i.e., about 75 eggs per female, while oviposition ceased about one month earlier (fig. 1). Possibly the fact that these females were more free to move about, caused them to be more prolific and they spent themselves faster and perhaps in the case with the isolated females the dim light affected their fertility.

A third series of nine pairs of *Baris* from the same lot was isolated on a water-melon and placed in a cellar with a dim light and a temperature of 22°C.

Under these conditions egg-laying ranged from 5–47 per female, the average being 17.

That *Baris* is capable of laying at low temperatures was demonstrated when 10 pairs were isolated and placed in a dimly lit cellar at a temperature of 15–17°C. Egg-laying continued for about one month, and on average some 3.5 eggs were laid by each female.

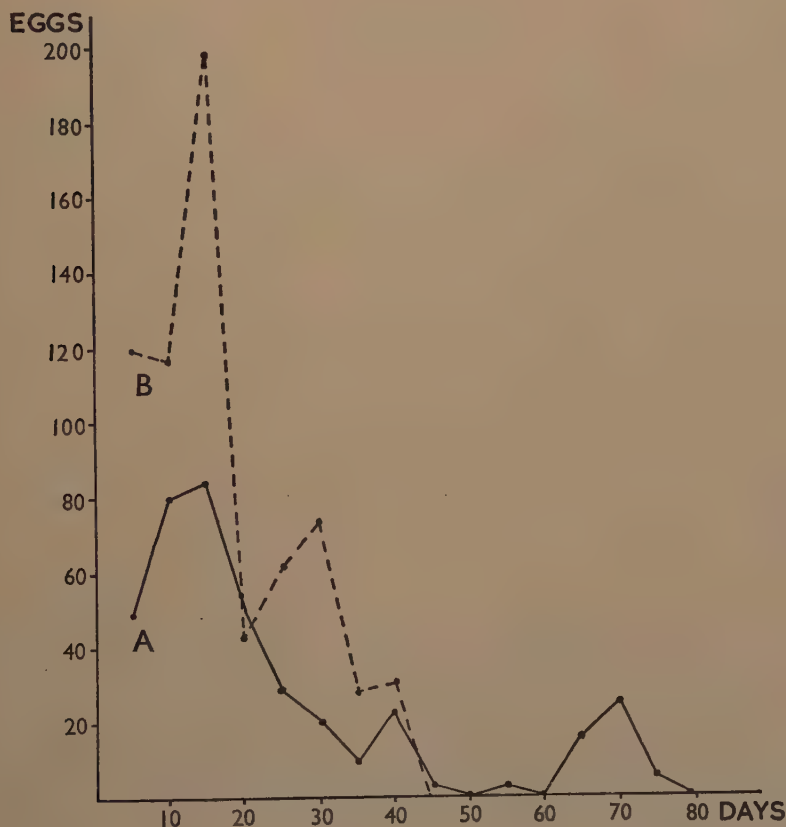


Fig. 1.—Rate of oviposition of *Baris granulipennis*. Eggs laid by:
A, 9 females in individual tubes; B, 9 females in one container.

From studies of other weevils it may be surmised that *Baris* weevils which have overwintered and weevils of the first generation probably lay more than the second generation, but this remains to be studied. Third-generation weevils, which emerged from their pupal cocoons early in October, laid few eggs. Because of the lack of fruits—water-melons or cucumbers—during October and November, no systematic study of their laying was made.

Length of life of adults.

The length of life of first- and second-generation weevils is presented in fig. 2. For the first generation the length of life of the 32 females and the 40 males is given separately. It is noticed that females lived a little longer than males. The oldest of both sexes lived 60–80 days.

In the second generation, no marked difference was noticed between length of life of males and females, so that the line represents the life of the entire 70 weevils, 35 from each sex. As noticed, there is also no marked difference in the length of life between generations. Weevils of the second generation, when placed at a temperature of 17 or 22°C. usually lived more than two or three

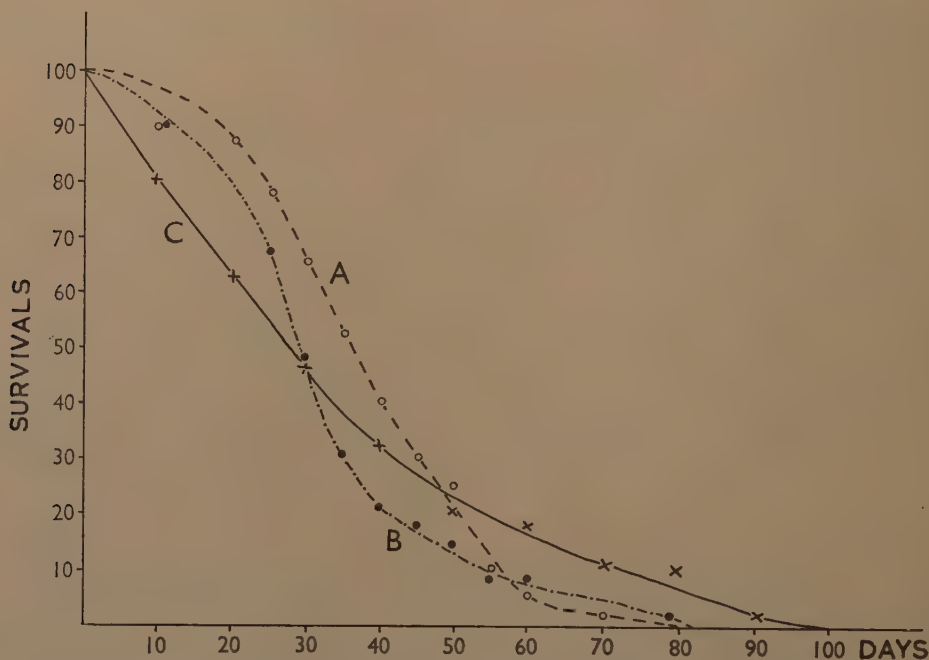


Fig. 2.—Length of adult life of *Baris granulipennis*. A, females of first generation; B, males of first generation; C, males and females of second generation.

months, while others went into hibernation. Those which emerged late in the season also hibernated, as did weevils of the third generation. A very few females, however, laid some eggs before doing so.

Number of generations.

The earliest infested fruit ever brought into the laboratory from the field was 30th May 1953. The infested melons and cucumbers showed fresh oviposition holes with unhatched eggs, which indicated that the attack occurred during the last week of May, *i.e.*, the weevils were already active in the field by mid-May. At this time, early melons and cucumbers are available. In June, water-melons also become abundant. The offspring of these—the first generation—should appear by the end of June, the second generation by the end of July and the third by the middle of September. Field observations support this estimate.

Oviposition in the field was observed by the writer as late as September. In fact the first weevils recorded in Israel were from eggs laid in late September or early October. In the laboratory, weevils of the second generation which emerged from their pupal cocoons on 19th September laid as late as the last week of October. Weevils of the third generation, which emerged on 2nd October, laid

as late as the third week of November. Twenty weevils which were brought as larvae from the field and emerged on 19th October, laid between them 3 eggs only, in the middle of November, before they hibernated.

Hibernation.

To some extent weevils of the third generation lay eggs. However, this activity was found to depend upon the date of emergence from their pupal cocoons. Thus, 21 weevils which emerged on 23rd September laid 21 eggs (room temperature 23°C.) and 24 weevils which emerged on 2nd October laid 84 eggs in the incubator (at 26°C.). On the other hand, 21 weevils of the same generation, which emerged on 19th October, failed to lay outdoors at a temperature of 21°C., while another 21 weevils of the same lot laid 3 eggs in the room at a temperature of 22°C.

Egg-production of second-generation weevils diminished greatly the later the date of emergence. Decreasing temperature was not the main factor as already noted, weevils of the second generation laid freely at a temperature of 22°C. and even at 17°C. Therefore, the reduced rate of oviposition would seem to be obligatory rather than facultative and presumably results from retarded development of the reproductive organs, of which the rate of maturation is dependent upon the emergence date.

Quite possibly only a small percentage of the third-generation females laid, as in the case with other species of weevils, but this remains to be studied further.

The percentage of survivals from the long hibernation depends upon the generation to which the weevils belong, and their age. Of three groups of weevils, which went into hibernation towards the end of November and which were examined early in March, the following were the results:

Of 25 second-generation weevils, which emerged on 11th August, none survived. Of 34 third-generation weevils, which emerged on 3rd October, six survived, while of 41 third-generation weevils, which emerged on 19th October, 22 survived.

Economic importance.

If it be assumed that the weevil is of local origin and has always existed in Israel, the question arises what brought about the sudden increase in population of this insect.

The answer could well be overabundance of food. In this country, water-melons and melons used to be grown without irrigation, so that soft young fruits suitable for oviposition were available only in June and July. This was the case with cucumbers too, even when grown under irrigation. In other words, there was food for overwintering and first-generation weevils. Food became scarce for the second generation and was still less available for weevils of the third generation.

As shown from this study, very few weevils of the second generation could survive the long hibernation period.

Today, with the enlarged areas under irrigation, water-melons are available on large areas at various dates in the summer; melons and cucumbers are also found throughout the summer, until late in October, and under such conditions third-generation weevils have a better chance of survival.

If it be assumed that the insect has been introduced, it might reasonably be postulated that it is these conditions which have enabled it to assume greater importance than at any time in its original habitat.

Summary.

Baris granulipennis (Tourn.), originally described from Egypt, has become a serious pest of water-melons (*Colocynthis citrullus*) in Israel, where hitherto its

presence has not been recorded, and has been found on melons and cucumbers, but not on vegetable marrow or squash. Economically serious damage results from girdling of the stem end of the fruit by the female, prior to oviposition.

The incubation period of the egg, on average, is 3.7 days at 30° and 6 days at 22°C. The larvae feed on developing seeds inside the fruit and pupate there. The total development period occupied from 25 to 42 days in the summer, when the temperature fluctuated between 24 and 29°C. The cocoon is made by glueing minute pellets together. These consist of dried pulp from the fruit mixed with a secretion which is 'milked' from the anus, and is believed to be produced in the Malpighian tubules. The preoviposition period is about four days, and the length of adult life is several weeks. There are three generations a year, and four if weather permits. Adults overwinter in hibernation. It is suggested that the increase of cucurbit cultivation, and the lengthening, by irrigation, of the cropping period, may have permitted an increase in the weevil population to pest proportions.

References.

- ADAIR, E. W. (1917). Additional notes on some Egyptian Cerambycidae mentioned in Mr. Alfieri's list.—*Bull. Soc. ent. Egypte* **10** pp. 96–97. (*Rev. appl. Ent. (A)* **6** p. 557.)
- BODENHEIMER, F. S. (1930). Die Schädlingsfauna Palästinas.—*Monogr. angew. Ent.* no. 10, 438 pp.
- BODENHEIMER, F. S. (1935). Animal life in Palestine.—506 pp. Jerusalem, L. Mayer.
- BODENHEIMER, F. S. (1937). Prodrusus faunae Palestinae.—*Mem. Inst. Egypte* **33** 286 pp.



FIG. 1. Three young water-melon fruits infested with *Baris* eggs ($\times 1$).



FIG. 2. A water-melon infested with larvae of *Baris*. The oviposition cavities in the peel and the spongy content should be noted ($\times \frac{1}{2}$).

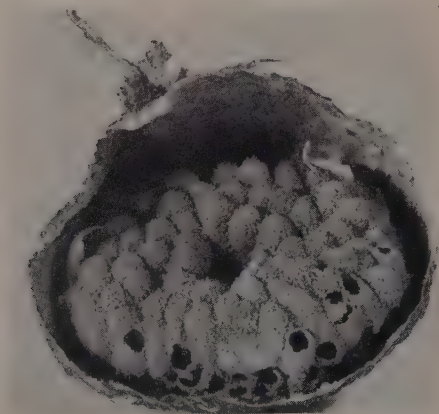


FIG. 3. Pupal cells of *Baris* in a shrunk dried water-melon fruit. Some of the cells have been evacuated by the beetles. From others, weevils are in the process of emerging ($\times \frac{1}{2}$).

THE CONTROL OF BLACK SAGE (*CORDIA MACROSTACHYA*) IN
MAURITIUS: THE INTRODUCTION, BIOLOGY AND BIONOMICS
OF A SPECIES OF *EURYTOMA* (HYMENOPTERA,
CHALCIDOIDEA).

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With an Appendix, on the present ecological status of *Cordia macrostachya*
in Mauritius, by P. O. WIEHE, C.B.E., D.Sc.

Director, Mauritius Sugar Industry Research Institute.

(PLATE VI.)

The control of the weed *Cordia macrostachya* (Jacq.) R. & S. in Mauritius is now a fairly well known example of successful biological control. Reference is made to Williams (1954) for both a short, comprehensive, account and for a list of the main publications on the subject. The present paper deals with a phase of the control work which has not previously been adequately described and includes data hitherto unpublished or published in fragmentary form in reports of the Mauritius Department of Agriculture.

C. macrostachya is a hardy shrub indigenous to Central America and the Caribbean Islands. It is known as the black sage and as 'herbe condé' in Trinidad and Mauritius, respectively. The major weed problem to which it gave rise in Mauritius was solved eventually by the introduction, effected with the aid of the Commonwealth Institute of Biological Control, of two phytophagous insects from Trinidad. The first, *Schematiza cordiae* Barber (Col., Galerucid.), is a leaf-feeding beetle which was released in Mauritius in March 1948, and by 1951 had solved the *Cordia* problem in a spectacular manner by killing the scrub through defoliation. The second, a species of *Eurytoma* which destroys the seeds, is the subject of the present paper. Following its establishment in Mauritius in 1950, it has supplemented the controlling action of *Schematiza*.

The introduction of *Eurytoma* into Mauritius.

A variety of small Hymenoptera infests the fruits of *C. macrostachya* in its native habitats, and from the outset of the control project the introduction into Mauritius of a seed-destroying species was considered highly desirable. The critical preliminary task was the selection from among the fruit-infesting species of a phytophagous form which would be suitable for that purpose. This was accomplished by Dr. F. J. Simmonds at the Trinidad station of the Commonwealth Institute of Biological Control, who determined the phytophagous rôle of *Eurytoma* sp. near *howardi* D.T.¹ Dr. Simmonds then began to collect *Cordia* fruits for dispatch to Mauritius and meanwhile forwarded specimens of the *Eurytoma* to

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¹ Specific identity is uncertain owing to the poor definition, by present standards, of many species of the genus.

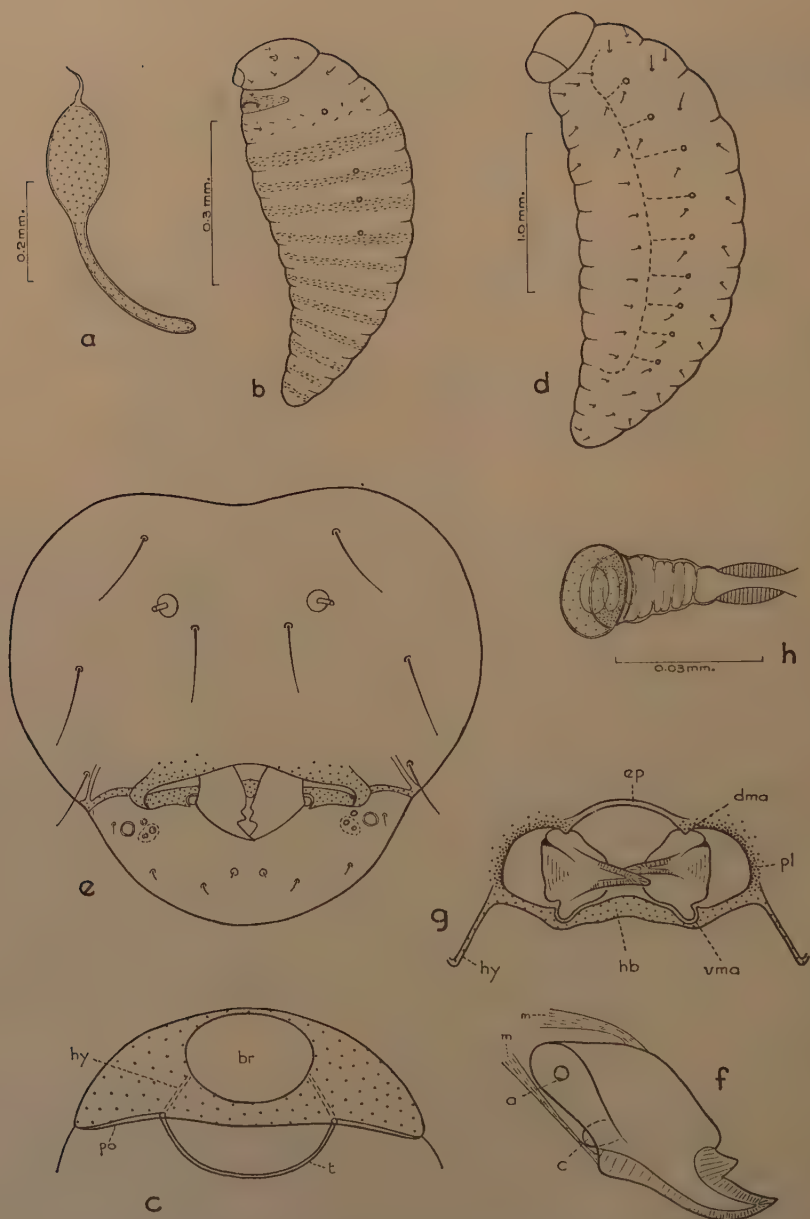


Fig. 1.—*Eurytoma* sp. nr. *howardii*: (a) ovarian egg; (b) first-instar larva; (c) same, diagrammatic view of head from below; (d) last-instar larva; (e) head of same; (f) mandible of same; (g) mouth frame of same; (h) spiracle of same. *a*, acron; *br*, buccal region; *c*, condyle; *dma*, dorsal mandibular articulation; *ep*, epistoma; *hb*, hypopharyngeal bracon; *hy*, hypostoma; *m*, muscle; *pl*, pleurostoma; *po*, postoccipt; *t*, tentorium; *vma*, ventral mandibular articulation.

enable it to be separated from the other species which would also emerge from the fruits after their arrival in Mauritius.

Between September 1949 and April 1950, a total of about 2½ million *Cordia* fruits were sent by air from Trinidad by Dr. Simmonds. The fruits were dried and treated with a fungicide before dispatch to prevent decay and heating in transit. Upon arrival in Mauritius, the parcels were opened in an insectary and the fruits quickly placed on wire trays within wooden cabinets which had a number of glass tubes inserted into holes in their sides. The insects which emerged from the fruits, being attracted to light, would collect in the glass tubes and from these they were removed daily for sorting.² The females of *Eurytoma* sp. nr. *howardii* and all males of *Eurytoma* were placed in jars or tubes with appropriate sugary food, and all other insects were killed immediately (separation of the males of the different species of *Eurytoma* was not possible with living specimens and was at no time attempted). The greatest care was imperative during the sorting to ensure that none of the unwanted species escaped or was inadvertently included with the *Eurytoma* in the jars. After retention for a few days, which served to build up the number available for each liberation and permitted mating, the *Eurytoma* were released upon *Cordia* bushes.

It should be noted that no tests for host-plant specificity were carried out with *Eurytoma* prior to its release in Mauritius. The insect's mode of development and close adaptation to its host-plant, described below, was sufficient guarantee of its specificity and harmlessness to other plants.

Considering the large number of *Cordia* fruits sent from Trinidad, the number of *Eurytoma* obtained for release in Mauritius was small, owing to the preponderance of other species in the fruits. Thus, between October 1949 and May 1950, only 1,300 females and 900 males had been released. However, by the latter date it was evident that the insect had become established in the locality where the first liberations had been made. The stock of Trinidad *Cordia* fruits was consequently destroyed to exclude all further possibility of the escape of undesired species.

Further colonies were established in various parts of the island with *Eurytoma* collected on *Cordia* at the first liberation site. By February 1951, about 6,500 adults had been so collected and distributed and at each liberation site the insect quickly established itself and could be easily recovered two or three months later.

Descriptions of the immature stages.

The ovarian egg (fig. 1, a). Colourless, without hairs or sculpturing. Ovoid, with a short, pointed, flagellum-like projection at one pole and a long tail or stalk at the other. The tail broadens slightly towards its extremity. Over-all length 0.6 mm., greatest width 0.12 mm.

The first-instar larva (fig. 1, b, c). Maximum size about 0.7 mm. long and 0.25 mm. wide. Whitish and translucent, with a head and 13 distinct body segments. Head much flattened, wider than long. Sclerotised, of a uniform light brown colour except for the darker pigmentation of the buccal region. Setae microscopic, the same in number and position as figured for the head of the last-instar larva. Hypostoma indistinct. Tentorium a slender and almost semi-circular strut (fig. 1, c). Body elongate, tapering posteriorly to a pointed

² Specimens sent to the Commonwealth Institute of Entomology for identification revealed the following species:

Eurytoma sp. nr. *howardi* D.T.
Eurytoma cressoni How.
Spilochalcis sp.
Torymus (*Syntomaspis*) sp.
Eupelmus sp.1.
Eupelmus sp.2.

Neocatolaccus sp.
Tetrastichus sp.1.
Tetrastichus sp.2.
Tetrastichus (*Galeopsomyia*) sp. ? *athenais* (Wlk.).
Tetrastichus (*Galeopsomopsis*) sp. nr. *valerus* (Wlk.).

extremity. First segment with a sclerotised ventral region which bears a pair of thickened ridges each shaped like half an ellipse with its concave face towards the posterior. Second segment with a few scattered minute spines. Remaining segments each with a complete band of minute spines. Setae microscopic, a dorsal and a ventral pair found on the first two segments; possibly there are more setae, but their size is such as to make their detection difficult among the spines. Tracheal system with spiracles on segments 2, 4, 5 and 6.

The first-instar larva fits well into Parker's (1924) Group VI of Chalcidoid larvae.

Head-width measurements showed that there are three larval instars between the first and the last. After the first moult, spiracles are also present on segments 3, 7, 8, 9 and 10, although in the second instar these spiracles are very much smaller than the primary spiracles.

The last-instar larva (fig. 1, d-h). About 3.0 mm. long when fully grown, tapering towards both extremities from about middle of body.

Head (fig. 1, e) unsclerotised except for buccal region. Rounded, with the face slightly flattened. Bearing four pairs of setae, each about 0.065 mm. long. Antennae cylindrical, 0.012 mm. long and 0.007 mm. wide, situated on broadly conical tubercles. Mandibles (fig. 1, f) 0.12 mm. long, heavily sclerotised, dark brown except for their bases, bidentate, with a lobe above the inner tooth and with a very prominent ventral condyle, articulated as shown in fig. 1, g. Epistoma not sclerotised. Hypopharyngeal bracon, hypostoma, and pleurostoma sclerotised, the brown colour of the latter merging gradually into the face. Labrum transparent, with a pair of setae on its outer surface (not shown). Ventrad of the mouth the head is produced in a membranous lobe bounded by the hypostoma and comprising the maxillae and labium. The maxillary regions are developed as smaller lobes and bear several sensoria which are well defined by their thickened rims (fig. 1, e). One sensorium is larger than the others and ovoid in shape, the two lower sensoria are on a common tubercle. Three pairs of setae are present in the maxillary-labial region, while there is also a pair of minute setae near the median line which have large thickened sockets. Body white and shiny. Chaetotaxy as shown in fig. 1, d. Thoracic setae about 0.1 mm. long, abdominal setae about 0.05 mm. long. There are no minute spines as in the first instar. Tracheal system with nine pairs of spiracles on segments 2-10. Those on 2 and 3 are ventrad from the line of the abdominal spiracles. External diameter of spiracles 0.022-0.025 mm. The atrium of a spiracle is a conical tube divided into numerous chambers by invaginations of its wall into septa, these chambers are often subdivided by smaller invaginations (fig. 1, h).

Adult biology.

Mating may occur immediately following emergence from the *Cordia* fruits. The male mounts on to the back of a female and bends its antennae sharply downwards. It then lowers and raises the front part of its body so that the curved antennae rub those of the female. The male becomes excited after a while and, moving backwards, curls its abdomen under that of the female and copulation occurs. A receptive female stands motionless, others continue to move about, ignoring the male, which falls off when attempting to copulate.

A newly emerged female has about 12 fully developed eggs, there being 1-4 in each ovariole, of which there are three to each ovary. The maximum number of eggs found in a newly emerged female (10 dissected) was 17 and the minimum eight. The eggs are arranged in the ovaries with their stalks uppermost, *i.e.*, directed towards the germinal filaments. The number of ripe eggs does not appear to increase when females are retained in captivity and fed with honey in water.

Virgin females oviposit readily. This was tested by placing unmated females

of various ages in muslin bags over *Cordia* inflorescences which were free from infestation. The resulting progeny were all male.

The average length of life of adults confined in jars with honey in water (mean room temperature 25°C., R.H. 75% approx.) was 11 days and 20 days for males and females, respectively.

Development.

The entire development of *Eurytoma* takes place within *Cordia* fruits, the structure of which is illustrated in fig. 2, while the different stages of fruit

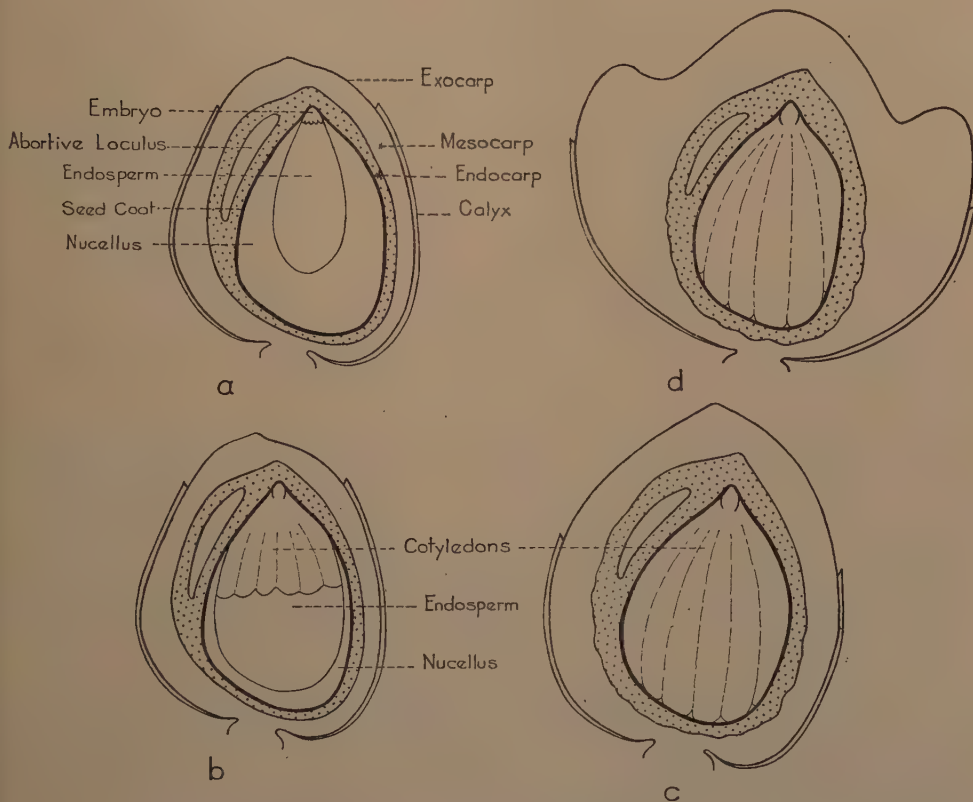


Fig. 2.—Stages in the development of a fruit of *Cordia macrostachya*. At (a) the endocarp is soft; at (b) it is beginning to harden; at (c) it is hard, and the mesocarp, although it has thickened to some extent, is still green; at (d) the fruit is ripe and the mesocarp is soft and fleshy and of a deep red colour.

development upon the inflorescence are shown in Plate VI, fig. 1. The ovary of a *Cordia* flower is syncarpous with four loculi, each containing one ovule. One to three, usually three, of the ovules abort, so that most mature fruits are one-seeded. This was illustrated by the dissection of 500 well-developed fruits; 88 per cent. possessed one seed, while 10.8, 1.0 and 0.2 per cent. possessed two, three and four seeds, respectively. The pericarp of a mature fruit is typical of a drupe, the endocarp being very hard and stony and the mesocarp soft and fleshy. The

final stage in the maturation of a fruit is the swelling and softening of the mesocarp and its change in colour from green to dark red.

A fruit is attacked before the endocarp hardens and generally when it has developed to a stage when it protrudes from the persistent calyx (fig. 2, a). The ovipositor is inserted into the fruit and an egg is laid against the inner surface of the seed coat. Less frequently the egg may be placed more deeply, so that it is enveloped by the gelatinous seed tissues. The stalk of the egg shrivels after deposition and remains trailing in the puncture made by the ovipositor through the pericarp. The young larva feeds upon the gelatinous nucellus and endosperm and later upon the cotyledons as these increase in size at the expense of the gelatinous tissues and descend into the body of the seed (fig. 2, b). The attacked fruit continues to increase in size, and its endocarp hardens, until it reaches the full size attained by a green fruit (fig. 2, c). At this point, development stops. The larva is now fully grown and the entire seed except for the seed coat has been consumed. The pericarp of an infested fruit therefore never becomes red and fleshy as shown in fig. 2, d. (Examples of infested and normal mature fruits are shown in Plate VI, fig. 2.) The larva now passes excrement for the first time and the entire gut contents are expelled as black ovoid pellets which stick together in a compact mass. In addition to the faecal pellets, the seed cavity at this time contains a ball of matter which is apparently detritus packed together by the larva. The seed cavity is thus clean, with two neat masses of waste matter when the larva is ready to pupate.

After emerging from the pupa, the adult insect remains in the seed cavity for one or two days, during which time the integument hardens. The insect finally bores through the enveloping stony endocarp, making an exit hole which is perfectly round and of a diameter just sufficient to allow its passage (Pl. VI, fig. 2).

An infested fruit frequently contains two or more young larvae. Sometimes all are healthy but often only one is alive and the others are dead and shrivelled. On one occasion, when two young larvae were dissected from a seed, one of the larvae had its mandibles inserted into the other and could be observed sucking out the body fluids. Only a small percentage of the many fruits dissected were found to contain two mature larvae, or two pupae, within the same seed. It appears that, when two larvae occur within the same seed, one kills the other when, as they increase in size, they eventually meet. This is an interesting homology with the activity of many entomophagous insects when superparasitism occurs.

The duration of development from egg to adult is about 23 days in the hot season.¹ During the cooler months of June–September, the last-instar larva has a resting period which appears to be of variable duration and the preimaginal period may last several months, and of this the pupal stage occupies only a very small part. This resting stage occurs usually after the gut contents have been voided. The duration of development up to the last larval instar varies little, irrespective of the season, and is about 15 days. Development to this point is, as described above, coincident with that of the fruit to the ‘hard green’ stage and in the cool season the growth of the fruit from the time when it is liable to infestation to the hard green stage is lengthened only by a matter of days.

When development of *Eurytoma* is not lengthened by a resting period in the last larval instar, attacked fruits are still attached to the flower stalk when the adult insect emerges. It is therefore common in the hot season to see green fruits with the round exit holes of the insect. When the mature larva becomes dormant, however, the green fruit dries and usually falls to the ground before emergence of the adult.

¹ Mauritius has two distinct seasons. The hot season from November to April and the cool season from May to October.

Bionomics.

At Réduit, where the first colony of *Eurytoma* was established in 1949, observations showed that the adults became comparatively scarce in the cool season. This is attributable to the resting period which occurs in the last larval instar during this season. In October 1950, fortnightly estimates of fruit infestation were begun in this locality and continued for 12 months. The method adopted was to take at random 100 hard green fruits from within about 100 yards of a given point and to split them open. Only those containing larvae visible to the naked eye were recorded as infested. Fruits were recorded as uninfested if no larvae were visible, provided that they contained viable seeds with fully, or nearly fully, developed cotyledons, otherwise they were rejected from the sample and others taken to replace them. Attacked fruits with easily seen larvae are normally beyond the stage when gelatinous tissues predominate in the seed, so that the estimates of fruit infestation related to fruits which (a) were at about the same stage of maturity—that subsequent to the development of the cotyledons when larvae, if present, are obvious—and (b) would not have been liable to further infestation if left in the field, owing to their hard endocarps.

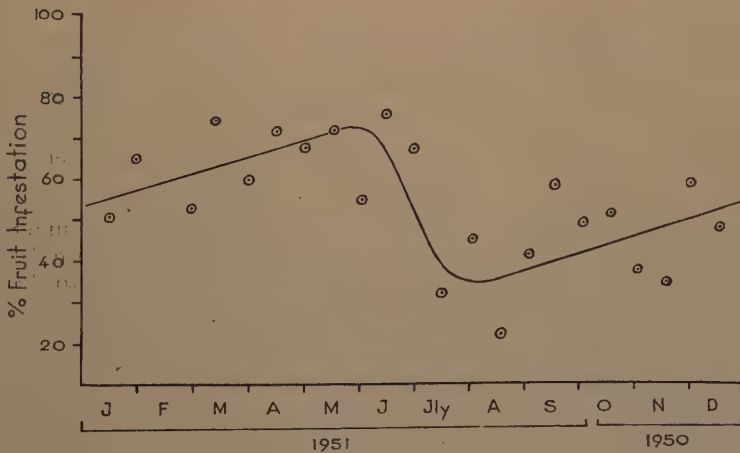


Fig. 3.—Infestation of fruits of *Cordia macrostachya* by *Eurytoma* at Réduit, 1950–51.

The results, which are plotted in fig. 3, showed a high average monthly infestation (53%) and a sharp drop in the degree of infestation in July, followed by a gradual build-up in succeeding months. The percentage of fruit infested at any given time is, however, inadequate in itself as a criterion of the insect's activity and beneficial action for the abundance of fruits varies considerably at different periods of the year.

Quantitative data upon fruit production of *Cordia* in the same locality have been given by Wiehe (1946) and fig. 4 is derived from his Table III, which gives the monthly production of inflorescences per bush. Other data which he gives show that the average time taken for an inflorescence to produce ripe fruits is about $2\frac{1}{2}$ months. The graph was accordingly constructed by plotting each monthly figure for inflorescence production with a $2\frac{1}{2}$ -month delay, i.e., Wiehe's 73 inflorescences produced in January is plotted as 73 inflorescences with ripe fruits in mid-March. The resulting graph is sufficient to illustrate the influence

of the seasons upon the fruit production of *Cordia* even though it omits the fact, also shown by Wiehe, that there are more fruits maturing per inflorescence, as well as more inflorescences, during the warmer months.

The following conclusions are to be drawn from the data in figs. 3 and 4. The seasons have a similar influence upon the reproductive rate of both the insect and the plant. The production of fruits increases throughout the summer months and likewise the percentage of infested fruits increases. When, during the cooler

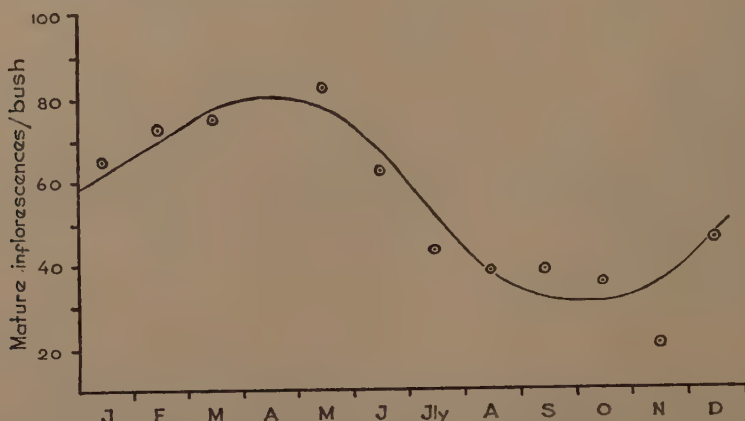


Fig. 4.—Seasonal trend of fruit production of *Cordia macrostachya* at Réduit (derived from data given by Wiehe, 1946).

months, fruit production is at its minimum, the last-instar larva undergoes a resting stage which reduces the population of adult insects to such an extent that despite fewer available fruits the percentage which are attacked falls to its lowest level. From the economic point of view, the insect is most efficient as a control agent during the hot season when the plant tends to be in full vigour.

The activity of *Eurytoma* in the island generally was assessed in October 1951, by estimating fruit infestation, in the manner described above, at or near the various points of liberation. Of 22 such estimates from different localities, the minimum infestation was 16 per cent. and the maximum 81 per cent., with an average infestation of 53.7 per cent.

The latest island-wide estimate of fruit infestation was made in 1953, when the average infestation calculated from about 25 samples from different localities in February, June and October was 64.6, 40.8 and 48.7 per cent., respectively.

Natural enemies.

Eurytoma in Mauritius is free from specific natural enemies. On a few occasions, however, black ants (*Technomyrmex detorquens* (Wlk.)) were seen to interfere deliberately with females attempting to oviposit. The ants, which are not predacious, grasped the female *Eurytoma* and a short struggle ensued, after which the *Eurytoma* escaped without having oviposited. The ants may be numerous on *Cordia* inflorescences, particularly when tending *Aphis gossypii* Glov., and it is possible that their presence protects a number of fruits from attack.

Discussion.

Owing to the uninhibited and very high rate of production of *Cordia* seeds in Mauritius (Wiehe, 1946), those connected with the *Cordia* control project during

its early stages favoured the employment of insects which directly reduce the plant's reproductive rate. Leaf-feeding insects were, nevertheless, the first to be introduced and a high degree of control was achieved by *Schematiza cordiae* in a surprisingly short time without the assistance of other insects. *Eurytoma* in Mauritius began to destroy appreciable numbers of seeds in 1951 only, when much *Cordia* scrub had been killed and was disappearing from *Schematiza* attacks. It may therefore be asked to what extent does the present control of *Cordia* depend upon *Eurytoma* and would control be any less satisfactory had *Eurytoma* not been introduced? The question cannot be answered satisfactorily. The two insects now act in unison and, it may be noted, without competing directly with each other. It is possible that, had *Eurytoma* not been introduced, the higher reproductive rate of the plant consequent upon its absence would have been balanced by a correspondingly greater activity upon the part of *Schematiza*, for the population level of this insect in Mauritius seems governed primarily by its food-plant density. On the other hand, it is reasonable to suppose that the presence of two very active and unrelated insects confers a greater stability to the control than would have been achieved by one insect.

Summary.

An account is given of the biology of the phytophagous Chalcidoid, *Eurytoma* sp. near *howardi* D.T., and of its bionomics in Mauritius. The insect was introduced into Mauritius from Trinidad to supplement the activity of the Galerucid beetle, *Schematiza cordiae* Barber, in the control of *Cordia macrostachya*, an introduced shrub, indigenous to Central America and the Caribbean Islands. The egg and larval stages are described and figured.

The entire development of *Eurytoma* takes place within the fruit of *Cordia*, which contains usually only one seed when mature and has a very hard and stony endocarp and a soft and fleshy mesocarp. Oviposition by *Eurytoma* takes place before the endocarp hardens; the egg is laid inside the seed and the larva feeds on the nucellus and endosperm and later on the developing cotyledons, until the entire seed, except for the seed coat, has been consumed. The attacked fruit continues to grow and its endocarp hardens, but final swelling of the mesocarp does not take place. Although more than one egg may be laid in a seed, only a small percentage of the many seeds dissected contained two mature larvae or two pupae. Pupation takes place within the seed, from which the adult escapes by boring a round hole through the endocarp.

Development from egg to adult occupies about 23 days in the hot season (November–April), but in the cooler months (June–September) the fully-grown larva enters a resting period, which may last several months.

Adults kept in jars, and provided with honey in water, at a mean temperature of 25°C., lived for an average of 11 days (males) or 20 days (females). A newly emerged female contains about 12 fully developed eggs. Virgin females oviposit readily, all the progeny being male.

Releases of adults from material received from Trinidad were made between October 1949 and May 1950; by the latter date it was evident that the insect had become established at the first liberation site and further colonies were established in various parts of the island from material collected there. Estimates of infestation of samples of fruit collected in October 1951 at or near 22 liberation points ranged from 16 to 81 per cent. (mean, 53.7). The latest island-wide estimates, in February, June and October 1953, showed averages of 64.7, 40.8 and 48.7 per cent. infestation, respectively.

Infestation of fruits is highest (70–80%) in the hot season, when fruit production is at its maximum, and lowest in the cooler months, when, although the rate of fruiting declines, the life-cycle of *Eurytoma* is prolonged.

Schematiza cordiae had achieved a high degree of control of *Cordia* before *Eurytoma* became widely established, and it is difficult to assess the contribution made by the latter, which has no known specific natural enemies in Mauritius; but the two unrelated insects acting jointly are likely to stabilise control more effectively than would one insect alone.

In an appendix, P. O. Wiehe gives notes on the present ecological status of *Cordia* in Mauritius and contrasts it with that prevailing before the introduction of *Schematiza* and *Eurytoma*. He concludes that the secondary succession of vegetation has now reverted to its former course.

References.

- PARKER, H. L. (1924). Recherches sur les formes post-embryonnaires des Chalcidiens.—*Ann. Soc. ent. Fr.* **93** pp. 261–379.
- WIEHE, P. O. (1946). Report on a visit to Trinidad, Louisiana and other countries. Part I. The control of *Cordia macrostachya* (Jacq.) Roem. and Schult. (herbe condé).—*Publ. Mauritius Govt.* no. 28 pp. 11–43.
- [WILLIAMS, J. R.] (1954). Mauritius. Review of agricultural entomology during the period 1948–1954.—*Rep. 6th Commonw. ent. Conf.* 1954 pp. 281–284.

APPENDIX.

The possibility of controlling *Cordia macrostachya* in Mauritius by biological means was first raised in 1939 by the late Mr. G. E. Bodkin, then Director of Agriculture, Mauritius. World War II deferred positive action upon the idea, but in 1945 Wiehe made the botanical and ecological study of the plant in the Antilles and Mauritius which led him to conclude that control of the plant in the latter might logically be approached by the introduction of its insect enemies. The entomological work involved was then pursued jointly by the Mauritius Department of Agriculture and the Commonwealth Institute of Biological Control, while the Imperial College of Tropical Agriculture in Trinidad also assisted in the early stages. In view of the successful outcome of the project it is appropriate that the present ecological position of *Cordia* in Mauritius should be briefly described, and at the request of the writer Dr. P. O. Wiehe kindly provided the notes given below.

Notes on the present ecological status of *Cordia macrostachya* in Mauritius.

By P. O. WIEHE, C.B.E., D.Sc.

Director, Mauritius Sugar Industry Research Institute.

The ecological position of *Cordia macrostachya* in the secondary vegetation of Mauritius prior to the introduction of some of its natural enemies from the West Indies was fully studied as part of the project for the control of this plant (Wiehe, 1946).

Less than 20 years after its introduction from British Guiana (circa 1890), *C. macrostachya* was firmly established as a weed in Mauritius. It encroached gradually on the secondary vegetation to become an exclusive dominant of large areas of grassland and scrubland under a wide range of rainfall conditions (30" to 100" per annum). The weed developed equally well on lithosols, latosols and hydromorphic soils. The aggressiveness of this new immigrant was due to a

variety of factors which favoured its unhindered growth, reproduction and spread. Of these, the absence of natural enemies was evidently of major importance.

The introduction from Trinidad of insects which feed only upon *Cordia macrostachya* and the successful establishment in Mauritius of two species, *Schematiza cordiac* Barber and *Eurytoma* sp., in 1948 and 1949, respectively, has already been described. It is of interest to record the position now occupied by *Cordia* a decade after the release of these insects.

Although scrubs composed dominantly of *Cordia* are still to be seen in certain localities, they are of small extent and show no tendency to spread. They are generally remnants of more extensive scrub which survived the sweeping early attacks of *Schematiza* and, probably owing to some favourable local combination of environmental factors, have been able to persist. Otherwise *Cordia* growths are not now dense and the plant is a subordinate constituent of the lowland scrubs and thickets of the island, including *Leucaena* scrub, *Litsea* thickets, and *Haematoxylon* thorn scrub. A distinguishing feature of these communities in former days was the almost impenetrable undergrowth formed by *Cordia*. This has now almost completely disappeared, *Cordia* being of comparatively rare occurrence and coexisting with other species of the same life form, such as *Lantana camara*, which are now able to compete successfully with it.

Similarly, on waste lands, along hedgerows, and on stone heaps in cane fields, where, for over a quarter of a century, *Cordia* was often the exclusive dominant, its status has now been relegated to that of an occasional species.

Finally, the grasslands that occur around the coast and in parts of the uplands of the island are now almost free from *Cordia*.

It may be concluded, therefore, that the secondary succession of vegetation has now reverted to its former course, biotic factors of animal origin (*Schematiza*, *Eurytoma*) having successfully controlled another biotic factor (*Cordia*), of vegetable origin, which had been responsible for the temporary diversion of the succession.



FIG. 1. *Cordia macrostachya*. Inflorescences of different ages, youngest on the left, oldest on the right; a few mature fruits are present on the latter ($\times \frac{3}{4}$).

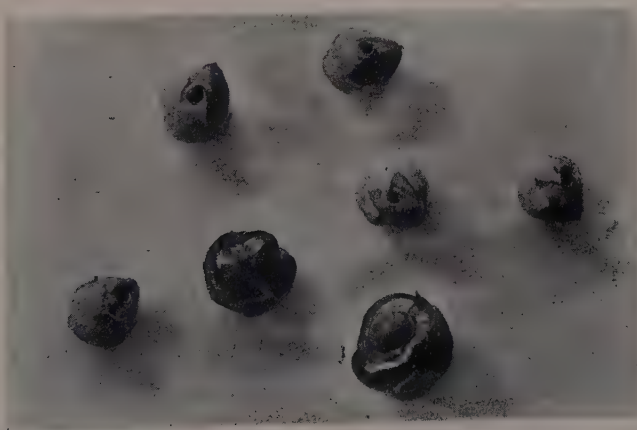


FIG. 2. *Cordia macrostachya*. Five green fruits showing emergence holes of *Eurytoma*, and two healthy mature fruits ($\times 2$).

AN INSECT-PROOF DOORWAY.

By B. HOCKING

E.M.N.*University of Alberta, Edmonton, Canada.*

It is not always convenient to use wire or fabric screening for the exclusion of insects from buildings, particularly where little if any insect entry can be permitted and where human traffic is heavy. These conditions require double doors and perhaps even the use of insecticidal sprays in between them. Two independent enquiries regarding the possibility of using air currents for this purpose led to this investigation.

Obviously, flying insects could be excluded by a current of air blowing outwards through the entrance at a speed equal to or greater than the maximum speed of flight of any insect species involved. An alternative possibility would be what is, in effect, a passageway, with a wind blowing across it at a speed greater in relation to its width than the maximum speed of flight in relation to its length. The first possibility presents mechanical difficulties, and since large department stores are important among potential users of the device, it has psychological drawbacks. The second possibility permits the use of lower air speeds, although correspondingly more air must be moved, and it offers other important advantages.

Assuming a rectangular cross-section, there are of course four directions in which the air current could blow across it, downwards, upwards, left to right, or right to left. Lateral movements offer no special advantages, whilst an updraught may have questionable entertainment value; evidence from other work (Hocking & Lindsay, 1958), however, suggests that a downdraught, especially if it carries a repellent odour, is likely to prove effective at speeds lower than those theoretically required. These investigations were accordingly all done with downdraughts. The results endorse this decision.

The theoretical requirements for insect exclusion, stated specifically for a downdraught, would be that the ratio of the air speed in the passageway to the maximum speed of flight of the insects should be greater than the ratio of the height of the passageway to its length. The honey bee may fly at air speeds up to 800 cm./sec. (Hocking, 1953) and blowflies at up to 400 cm./sec. (unpublished data) so that, with a passageway of the proportions indicated in the next section, air speeds of the order of 2160 cm./sec. ($800 \times \frac{1}{0.37}$) and 1080 cm./sec. would

be needed to prevent honey bees and blowflies, respectively, from flying through.

Materials and methods.

Tests were conducted with a model passageway at one-quarter linear scale, 19.5 in. high, 4.5 in. wide, by 7.25 in. long; the ratio of length to height was thus 0.37. This was arranged between the square ends of two plywood cages with glass sides and 28-mesh saran screen tops, each measuring 3 ft. \times 2 ft., so that its floor was level with the floors of the cages (fig. 1). Sponge rubber gaskets, $\frac{1}{8}$ in. thick, gave an airtight and insect-tight seal between each cage and the passageway. It was found convenient to set this a few inches from one side of the cages rather than in the centre of the ends. Brackets for a roller blind were mounted externally, at floor level, at either end of one side of each cage. A dark blind long enough to cover the glass sides and screen top of the cage could be placed in either of these positions and unrolled to darken either cage

completely. A hole, $1\frac{1}{2}$ in. diameter, was drilled in the outside end of each cage, opposite the centre of the passageway, and covered with acetate sheet; all four walls of the passageway could then be observed through either of these holes.

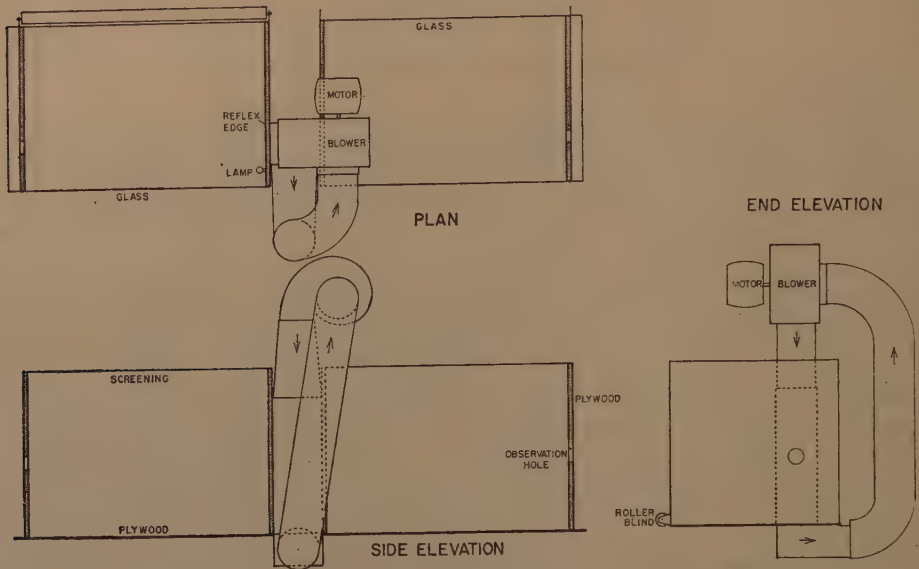


Fig. 1.—The arrangement of cages and experimental passageway.

The passageway (fig. 2) was built of $\frac{1}{2}$ -in.-thick fir plywood; one vertical wall was sanded smooth inside and the other was left rough. The floor and the ceiling were made of 20-mesh brass screening supported by bronze strips, 1 in. wide by $1/32$ in. thick, $\frac{3}{4}$ in. apart. These were transverse on the floor to represent a grating and longitudinal on the ceiling, where their purpose was to aid in straightening the air flow. Vertically upwards above the ceiling and laterally below the floor were tapered plywood sections to which the outlet and inlet respectively of a 6-in. centrifugal blower were coupled through sheet-metal stove-pipe and rubber connectors. The blower was mounted above the passageway and driven by an integral $\frac{1}{4}$ h.p. motor, the speed of which was controlled by a variable transformer. A Pitot tube was mounted with its dynamic pressure opening facing upwards in the geometrical centre of the passageway; an oil manometer at a slope of 10° was used with this. This arrangement had been previously calibrated against a hot thermopile anemometer.

Early in the work it became clear that insects crawling through the passageway might constitute the major problem. The effects of five factors on this were investigated. These were the structural and visual properties of the edges between the donor cage and the passageway (reflexed metal edges and illumination control) and of the walls of the passageway itself (rough, smooth, or shiny; plain or patterned) and the presence of an odour in the air stream.

The vertical edges were modified in two ways: firstly, by fitting them with bronze strips, $1\frac{1}{2}$ in. wide and $1/32$ in. thick, bent back at an angle of 45° to the end wall of the cage; secondly, by mounting tubular 60-watt filament lamps $17\frac{1}{2}$ in. long by 1 in. diameter (General Electric Lumiline) on the inside of the end wall of the cage, with centres 1 in. back from the edge of the passageway. The

nature of the surface of the sanded wall of the passageway was also changed by covering it with polished acetate sheet under which plain black or plain white cards or a white card with $\frac{3}{4}$ -in. black dots on it were placed. The opposite rough wall was left unchanged for comparison. The only odour tested was that of dimethyl phthalate. A 9-in. length of the return pipe of the air circulating system was loosely packed with wood-wool soaked in this liquid and then drained. The wood-wool was held in place by discs of $\frac{1}{4}$ -in. mesh heavy wire screen.



Fig. 2.—Detail of the experimental passageway.

The insects used in most of the tests were the house-fly, *Musca domestica* L., reared by the method described by Fisher & Morrison (1950), and the honey bee, *Apis mellifera* L. (field-age Italian workers from a laboratory observation hive); a limited number of confirmatory tests were run with *Drosophila melanogaster* Mg., reared on a standard maize-meal medium, and field-trapped adults of the Chloropid, *Thaumatomyia glabra* (Mg.).

From 150 to 500 insects were used in each batch. These were admitted to one of the cages and the rate and manner of their passage through to the other cage was studied under various conditions of the passageway edges and walls and the air current. In order to accelerate the passage of the insects so that results could be obtained in a reasonable time, light intensity was controlled in the cages with the roller blind and with overhead fluorescent lights. Working with the honey bee, the donor cage was darkened and the recipient cage illuminated. With house-flies the reverse procedure was necessary. Using a mechanical counter with five separate keys and tallies and looking through the observation hole it was possible to record separately the numbers of insects flying into the passageway and the numbers crawling in on each of its four faces with good accuracy at total frequencies up to 2 or 3 per second. When the population density in the donor

cage became so low that further counting was not worthwhile, the blind and lighting were reversed and a count was taken in the opposite direction. A crawling insect was counted as having entered the passageway when all six feet had crossed the threshold at the donor cage side, regardless of the behaviour of the insect thereafter. Many insects of course crossed the threshold but failed to reach the other side. Some crossed and re-crossed the threshold several times; no attempt was made to discriminate between individual insects. It was not possible to be so precise with flying insects.

Temperature and humidity were recorded throughout the tests and ranged between 75 and 85°F. and 38 and 55 per cent. R.H. Food and water were available in both cages during all tests.

TABLE I.

The influence of air speed of a vertically downward wind on the number of insects flying per sq. m. and crawling per m. across the threshold into a plain passageway.

	Air speed (ft./min.)	0	500	1000	1500
<i>Apis</i> (450 insects/m. ²)	Flying/m. ² /min.*	48 ± 8.2 (4)	7.8 ± 1.7 (4)	1.1 ± 0.45 (10)	1.2 ± 0.52 (4)
	Crawling/m./min.*				
	Ceiling	14 ± 2.9	6.3 ± 0.82	5.3 ± 0.69	4.4 ± 0.51
	Wall	7.9 ± 1.4	7.7 ± 1.2	4.1 ± 0.58	2.3 ± 0.38
	Floor	33 ± 9.6	63 ± 14	29 ± 7.2	17 ± 4.2
	% on floor	60	81	77	72
<i>Musca</i> (1600 insects/m. ²)	Total crawling/m.	8.1	11	6.5	3.9
	Total entering**	158	100	44.5	28.3
	Flying/m. ² /min.*	62 ± 12 (4)	30 ± 6.3 (5)	4.5 ± 1.9 (10)	—
	Crawling/m./min.*				
	Ceiling	12 ± 2.5	13 ± 2.7	6.7 ± 2.1	—
Average of both species	Wall	3.0 ± 1.3	3.7 ± 1.9	4.6 ± 1.7	—
	Floor	29 ± 7.8	55 ± 14	44 ± 8.5	—
	Total crawling/m.	7.5	11	8.5	—
	Total entering**	171	135	68.5	—
	Flying/m. ² /min.	55	19	2.8	—
	Crawling/m./min.				
	Ceiling	13	10	6.0	—
	Wall	5.4	5.7	4.3	—
	Floor	31	59	36	—
	Total crawling/m.	7.8	11	7.5	—
	Total entering**	165	118	56.5	—

* Each result is shown as the mean ± standard error of the mean. The numbers of observations are shown in parentheses.

** By calculation from data above, on the basis of a hypothetical entrance, 2 m. high by 1 m. wide.

Results.

The first tests were designed to compare the effect of different air speeds on insects flying into the passageway. It was found possible, at the lower speeds, to record the effects on crawling insects at the same time. The results, expressed in numbers per square metre of entrance area or per metre of edge, are given in Table I.

With the honey bee, little further influence on the number of insects flying

TABLE II.

The influence of the mechanical and visual properties of the edges and walls of a passageway with a vertically downward wind on the number of insects crawling across the threshold into it per m. of edge per minute.

Air speed (ft./min.)		0	500	1000
Reflex edges \times plain edges				
<i>Apis</i> (c.450 insects/m. ²)	Reflex	1.3 ± 0.35 (4)	2.8 ± 0.74 (4)	1.1 ± 0.29 (4)
	Plain	7.9 ± 2.1 (4)	7.6 ± 2.0 (4)	4.7 ± 0.62 (4)
<i>Musca</i> (c.1600 insects/m. ²)	Reflex	3.0 ± 0.96 (4)	2.0 ± 0.61 (4)	1.2 ± 0.31 (4)
	Plain	3.8 ± 1.1 (4)	3.1 ± 0.92 (4)	4.7 ± 1.6 (4)
Illuminated edges \times reflex edges				
<i>Apis</i>	Illuminated	—	—	1.2 (2)
	Reflex	—	—	1.1 (2)
<i>Musca</i>	Illuminated	—	—	1.2 (2)
	Reflex	—	—	1.2 (2)
Shiny wall \times rough wall				
<i>Apis</i>	Shiny (white)	—	3.6 (2)	2.5 (2)
	Rough	—	5.7 (2)	3.4 (2)
	Shiny (black)	—	—	0.83 (2)
	Rough	—	—	2.3 (2)
Patterned wall \times plain wall				
<i>Apis</i>	Pattern	—	—	4.5 ± 1.1 (4)
	Plain	—	—	2.2 ± 0.61 (4)
<i>Musca</i>	Pattern	6.0 ± 1.9 (4)	7.4 ± 1.9 (4)	6.2 ± 1.7 (4)
	Plain	3.0 ± 0.92 (4)	3.7 ± 0.96 (4)	2.8 ± 0.72 (4)

across the threshold was manifest at wind speeds over 1,000 ft./min.; two tests were run, with a small number of insects, at a speed of 2,200 ft./min.; a few insects still flew across the threshold, but none got right through the passageway. Tests with the house-fly, and those tests of structural modifications using both insects, were therefore confined to air speeds from 0 to 1,000 ft./min. (508 cm./sec.), this being the highest speed at which useful counts could be obtained in a reasonable time.

Attention was then directed to the control of insects crawling through the passageway. The principal results obtained in these tests are given in Tables II and III. Observations with *Drosophila* and *Thaumatomyia* were insufficient for numerical presentation, but neither species showed any important difference in behaviour as compared with the honey bee and house-fly. Differences observed could be attributed to the size differences.

TABLE III.

The influence of the vapour of dimethyl phthalate carried on a vertically downward wind on the number of house-flies flying and crawling across the threshold into a plain passageway. Air speed, 500 ft./min., two sets of data.

	Clean air*	Dimethyl phthalate
Flying/m. ² /min. ..	30	28
Crawling/m./min.		
Ceiling	13	3.4
Wall	3.7	3.7
Floor	55	4.5
Total crawling/m./min.	11	3.7
Total entering** ..	135	77.5

* Data from Table I.

** By calculation from data above on the basis of a hypothetical entrance, 2 m. high by 1 m. wide.

Preliminary observations showed that more insects crossed on the rough plywood wall than on the smooth sanded wall. This led to the comparative tests of a smooth shiny surface with the rough plywood. With the honey bee, a white surface underlying the acetate sheet gave a reduction of 26 per cent. at an air speed of 1,000 ft./min.; a black surface gave 64 per cent. reduction. Rough tests with flies showed that the balance between black and white was the other way. This was expected from the different light reactions of the two insects.

Tests with a patterned wall were started in the expectation that good visual orientation would facilitate the response of flying insects to the adverse air current and thus permit a lower air speed to be used. This effect was found to be negligible; presumably features of the passageway itself were adequate for visual orientation. A marked increase in the number of crawling insects was found, however; at an air speed of 1,000 ft./min., this was 104 per cent. for the honey bee and 121 per cent. for the house-fly. Tests with other types of pattern showed that insects tended to follow lines of pattern into the doorway.

Tests with dimethyl phthalate, a widely used insect repellent, were conducted with house-flies at an air speed of 500 ft./min. to ensure that there would be an adequate number of insects flying into the passageway, since it was anticipated that the effect would be greatest on flying insects. Clearly this was not so. The

percentage reduction in the number flying in was only 7, the reduction in the number crawling in was 66 per cent. The overall reduction was 43 per cent.

In all tests except those with dimethyl phthalate, house-flies showed a tendency to form clusters in the corners of the passageway, especially those at the top. The most striking effect of the addition of dimethyl phthalate to the air stream was the breaking up and dispersal of these clusters. This process was usually complete in from 30 to 60 seconds. After tests with dimethyl phthalate the thigmotactic response of flies seemed to be accentuated; most of them clustered in the corners of the cages or in crevices between food and water containers.

When the air flow in the passageway was steady at high speeds, there was considerable overflow of air outwards along the floors of the cages. Nearly all flies standing on the floor faced into this air current. When the duct between the blower and the passageway was restricted or the blower slowed down so that the speed and extent of these outward currents were reduced, flies oriented in this way promptly walked forwards; a resumption of the original conditions stopped them.

The possibility of using air speeds high enough to prevent insects from crawling through the passageway on the smooth shiny walls was considered. Speeds up to 2,200 ft./min., however, were not effective, and it was felt that higher speeds would not be economic or acceptable to human users of a passageway. Although the bodies of insects subjected to these speeds were strongly deflected, their progress slowed, and some were blown off, many managed to complete the transit of the passage.

Discussion.

From Table I it is clear that there is no great problem in preventing insects from flying through a doorway. An air speed of 1,500 ft./min. at a length-to-height ratio of 0.37 seems to offer a satisfactory combination of efficiency with economy and acceptability.

The prevention of insects crawling through is more difficult and requires a combination of features. Examination of Table I shows that a downward air current of 1,000 ft./min. had no significant ($P = 0.05$) effect on the total number of insects crawling into the passageway, although it did have an effect on their distribution, increasing the number on the floor at the expense of the numbers on ceiling and walls. This is important. A removable floor grid or grating can readily be treated with a long-term residual insecticide, which will ensure that any insects passing through by this route will die within about 24 hours. In situations where no insecticide can be permitted, treatment with a low-friction finish such as 'Fluon' (Merton, 1956) should be satisfactory. The arrangement of other modifications may well be directed also to forcing insects to pass by the floor route.

While the effects of the different modifications of edges and walls are not strictly additive, there were indications, from the behaviour of both bees and flies in relation to the modifications, that the effects of applying these devices collectively should be very much greater than the effects of any one device. This applies particularly to the two most important devices, reflex edges and illuminated edges.

It should perhaps be repeated here that the figures in the tables represent numbers of insects crossing the threshold into the passageway. While it was not possible to count these, it may be said that of the insects entering the passageway on the wing, hardly any penetrated to the other side except at zero air speed; all of those which did so entered the passageway close to the ceiling. Most crawling insects, especially at the lower air speeds, eventually reached the other side; those that did not were mostly those that got into the floor grid.

It should be especially noted that the number of insects crawling into the passageway per unit time per unit length of edge is increased by one particular feature of wall surfaces, namely, the presence of conspicuous pattern. This has a very pronounced effect and may more than double the number of insects entering. Presumably pattern must be visible to insects from an appreciable distance to have this effect. It may be tentatively suggested that, taking the average angular resolving power of an insect compound eye to be 1° , any pattern subtending an angle of more than 1° at a distance of about $1/5$ th of the width of the entrance and with reflectivity differing markedly from the background within the wavelength range 2,600 to 7,000 ångströms would exert a significant effect.

The number of insects entering the passageway was found to increase very steeply with population density. There was some variation in population density in the tests; this was small between tests of any one feature or pair of features, as may be inferred from the small standard errors in these data. It may have been great enough between series of tests to render comparisons between features invalid. Such comparisons should be made with caution. The population densities outside the passageway which gave these results were, of course, of a higher order than anything that is likely to be encountered in practice, unless the device were to be used for insect-rearing rooms or cages. Here it would seem desirable to combine the device of an air current with that of a sliding door that switches on the blower and the lights as soon as it is opened. As an added precaution, a strip of low-friction finish might well be extended up the sides and across the top.

Examination of Table II shows that when combined with an air current of 1,000 ft./min., reflex edges reduced the number of insects entering the passageway by about 75 per cent. Similar edges fitted at the other end of the passageway may be expected to have a similar effect, giving a reduction of about 94 per cent. in the numbers completing the passage. It is difficult to use a reflex edge effectively at the floor of an entrance unless there is a step up, which is usually undesirable for other reasons, but this is immaterial if a residual insecticide is used.

The effect of an illuminated edge is seen to be similar in magnitude to that of a reflex edge (Table II). The expectation that the lighting would hold insects showing a photopositive reaction while the reflex edge would hold those reacting photonegatively or showing a thigmotactic response was supported by observations of the behaviour of insects towards these features. It follows that the lighting should be arranged in such a way that it does not shine behind the reflex strips.

While the addition of dimethyl phthalate proved a valuable contribution to insect exclusion and might be required in some circumstances, it is much more difficult to apply than the other features discussed, which can probably give adequate protection without it. It may also prove to be more specific than the other features, and may be without effect on some insect species.

The factors that reduce the number entering, while not strictly additive, can all be applied together, with the effect of reducing the number of insects crawling into a doorway to a very low level and the number of insects crawling through it to an even lower level. This remains highest on the floor.

There are grounds for suggesting that pronounced fluctuations in air speed should be avoided; those caused by people, or vehicles small in relation to the size of the doorway, are not likely to be harmful. It should be mentioned that insects on people, or in or on packaged goods, passing through the doorway are unlikely to be significantly affected. It also seems desirable to avoid any sort of obstruction on the suction side of the doorway air circuit; such obstruction would lead to an excessive outward flow of air from the doorway on either side, which has undesirable results.

The following seem to be the desirable features of an insect-proof doorway (see fig. 3):

(1) A vertical downward air current in the doorway of such dimensions that the product of the average air speed (in ft./min.) and the ratio of the distance through the doorway to its height has a value not less than 550. This figure is based on the speed of 1,500 ft./min. and the length/height ratio of 0.37, shown by the present work to be satisfactory.

(2) Walls and, as far as possible, ceiling and floor of material with a smooth shiny surface.

(3) The floor grid transverse rather than longitudinal, the spacing as great as possible consistent with the convenience of users.

(4) The combination of floor grid and screen readily removable for cleaning and for re-treatment with a long-term residual insecticide, such as a dieldrin lacquer.

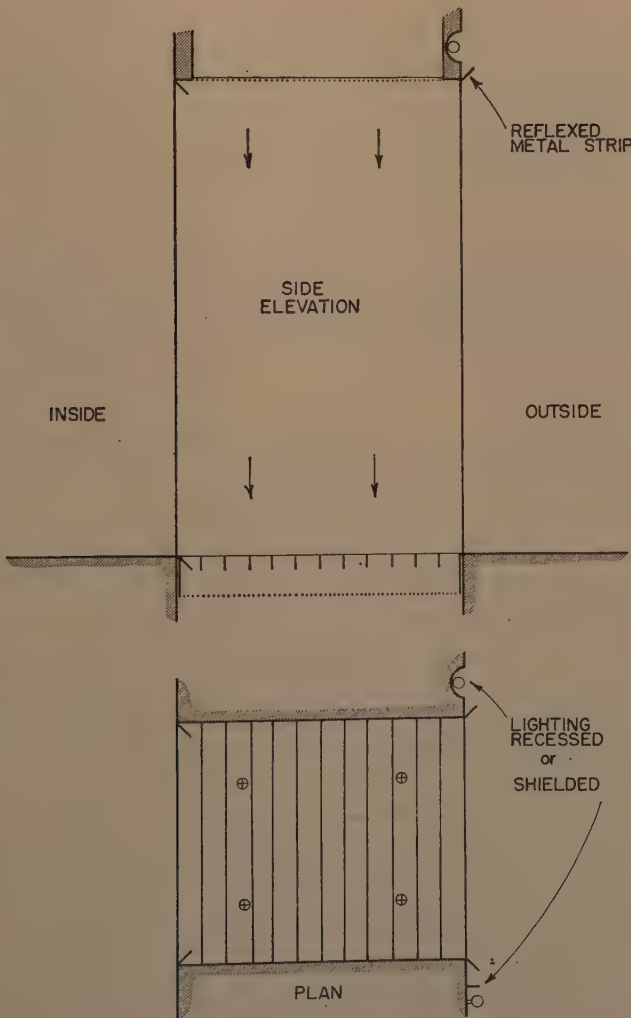


Fig. 3.—A suitable arrangement for an insect-proof doorway.

(5) The edges of the entrance fitted, top and sides, with 2- to 3-inch-wide metal strips inclined upwards and outwards, respectively, at 45 degrees; similar strips might with advantage be used on the edges at the other end of the doorway, inclined inwards, in relation to the passageway, on the sides, or downwards, at the top and bottom edges. Effective use of a reflexed metal strip at the outer edge of the floor can only be made if there is a step up, which may be unacceptable to users. The metal strips could, of course, be decorative.

(6) The entrance outlined by lighting, a few inches from the reflexed metal strips, and arranged in such a manner as not to shine into the angle subtended by them.

(7) No pattern visible to insects, and especially none with a linear structure leading through or into the doorway, as, for example, mortar joints in masonry of contrasting colour or a floor grid running through the entrance. A suitable arrangement is illustrated in fig. 3.

Summary.

The factors which influence the passage of flying and crawling insects through a doorway were investigated. It was considered practicable to exclude flying insects from a building or to prevent their successful escape from cages or rearing rooms by means of a downward air current if the speed of this in ft./min. multiplied by the ratio of the length through the doorway to its height is not less than 550. A combination of reflex and illuminated edges, smooth shiny walls without a pattern visible to insects, and a floor grid and underlying screening treated with a long-lasting residual insecticide, will, at all natural population densities, reduce to an insignificant level the number of insects that crawl through and survive. Artificially higher densities, as in rearing rooms, may require that the doorway be fitted with sliding doors in addition. These may be arranged to switch on the air current and lights as soon as they are opened.

Acknowledgements.

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References.

- FISHER, R. S. & MORRISON, F. O. (1950). Methods of rearing and sexing (*Musca domestica* L.).—*80th Rep. ent. Soc. Ont.* 1949 pp. 41–45.
- HOCKING, B. (1953). The intrinsic range and speed of flight of insects.—*Trans. R. ent. Soc. Lond.* **104** pp. 223–345.
- HOCKING, B. & LINDSAY, I. S. (1958). Reactions of insects to the olfactory stimuli from the components of an insecticidal spray.—*Bull. ent. Res.* **49** pp. 675–683.
- MERTON, Sir T. (1956). On a barrier against insect pests.—*Proc. roy. Soc. Lond.* (A) **234** pp. 218–220.

THE MOSQUITOS OF ZARIA PROVINCE, NORTHERN NIGERIA.

By P. W. HANNEY

CONTENTS.

	PAGE
Description of the investigation	145
Methods	147
Trap catches	147
Biting catches	147
Bionomics of the principal endophagous species of <i>Anopheles</i>	149
Seasonal fluctuations	149
Sporozoite rates	152
Times of entry into and departure from houses	152
Times of feeding inside houses	154
Preferences for indoor and outdoor feeding	155
Seasonal fluctuations in numbers of other prevalent species of <i>Anopheles</i> ...	158
Seasonal fluctuations in numbers of the principal nocturnal anthropophilous species of <i>CULICINAE</i>	159
Discussion	160
Summary	161
Acknowledgements	162
References	162
Appendix: A list of all species of ANOPHELINAE, <i>CULICINAE</i> and TOXORHYNCHITINAE recorded from Zaria province, with notes on their distribution and bionomics	163

Description of the investigation.

Kaduna, the capital of the Northern Region of Nigeria, is a town of 12 square miles extent with 44,500 inhabitants, situated at lat. 10°30'N. and long. 7°28'E., in an enclave of capital territory enclosed by Zaria Province. The studies described below, which were designed primarily to ascertain the bionomics of actual and potential vectors of malaria in the area, were carried out between June 1957 and December 1958, within a radius of 50 miles of Kaduna, during which time the mosquito population was kept under almost continual observation. As energetic control measures with larvicide were in force in Kaduna township, all the observations reported on bionomics were made outside the control zone. Short-term mosquito surveys have been made previously in the district by A. W. Brown, R. A. Fitzjohn and P. F. Mattingly (Malaria Service records) and records made by these and other workers are included in the Appendix.

The climate of Northern Nigeria is characterised by two well marked seasons, the wet season extending from April until October and the dry season from November until March. In Kaduna, the mean annual rainfall is 45 in., but further north precipitation is less, Katsina, 200 miles to the north, receiving 35 in. From December to February a strong NE. wind, the 'Harmattan', is experienced; since this often lowers the temperature at night to below 60°F., the daily temperature range during this period is often as much as 25°F. During the wet season, the prevailing winds are south-westerly, and the humidity rises considerably. During this period the mean minimum temperature at night is about 70°F., the daily temperature range being smallest between July and August when it is often less than 10°F. The maximum rainfall occurs in September.

The topography of the area is gently undulating with scattered granite outcrops; the altitude is about 2,000 ft. The vegetation is of the Guinea Savannah type. The region is traversed by numerous small streams which drain into the Kaduna river. A number of streams are bordered with fringing forest, where distinct and isolated mosquito communities occur. During the rains, flooding leads to the formation of small swamps.

TABLE I.

Meteorological records, Kaduna, 1958.

Temperature (°F.)						
	Mean max.	Mean min.	Range	Mean temp.	Absolute max.	Absolute min.
Jan. ..	90.9	64.6	26.3	77.4	100.0	56
Feb. ..	89.6	64.3	25.3	76.8	98.0	58
Mar. ..	97.5	72.0	25.5	85.0	101.0	65
Apr. ..	91.5	73.5	17.0	82.0	98.0	70
May ..	90.2	73.9	16.3	81.9	94.0	68
June ..	83.6	71.2	12.4	76.4	88.0	68
July ..	79.0	75.4	4.4	77.6	83.0	68
Aug. ..	79.9	70.4	9.5	75.1	88.0	67
Sept. ..	83.8	70.4	13.4	77.1	88.0	66
Oct. ..	89.5	71.7	17.8	80.6	93.0	68
Nov. ..	92.3	68.6	23.7	80.2	95.0	63
Dec. ..	92.6	64.2	28.4	78.4	98.0	59

	Humidity					Rainfall
	R.H.(%) at max. temp.	R.H.(%) at min. temp.	Range	Mean R.H. (%)	Mean daily evaporation (cc.)	Monthly (in.)
Jan. ..	35	48	13	41.5	96.4	0
Feb. ..	26	38	12	42.0	116.0	0
Mar. ..	27	41	14	34.0	115.9	0
Apr. ..	50	86	36	68.0	45.8	4.31
May ..	47	86	39	66.5	25.9	5.31
June ..	49	81	32	65.0	19.6	7.95
July ..	60	66	6	63.0	12.3	6.17
Aug. ..	72	90	18	81.0	12.3	8.38
Sept. ..	66	90	24	78.0	10.5	13.08
Oct. ..	49	86	37	66.5	31.2	7.56
Nov. ..	50	81	31	65.5	58.16	0.03
Dec. ..	32	65	33	48.5	90.85	0

The rural population is gregarious and lives in villages of varying sizes. It is mainly agricultural, and farming activities provide many additional mosquito breeding places. The mud huts in which the people live are mostly rectangular, about 180 sq. ft. in area, with thatched roofs; windows are lacking, and the doorways are covered at night with grass mats. The huts are never completely subdivided into rooms. Domestic animals include goat, sheep, dog and fowl which are generally loose in the compound, which surrounds the house, but occasionally share the hut of their owner. The inhabitants of the villages in which the observations were made generally sat outside their huts until about 10.0 p.m. before retiring. An average of 2.6 persons sleep in each hut; this differs from the custom in round huts in the Sokoto area, where 1.0-1.5 persons occupy a hut.

Malaria is holoendemic throughout Nigeria but in the Kaduna area, as indeed throughout the Northern Region, there is an increased incidence in the wet season. However, at the height of the dry season (January-February) in 1958 the bloods of 200 children aged up to 10 years and living in mosquito observation villages were examined for malarial parasites. Eighty-seven per cent. of the total were found to be positive, but in two small villages all were infected.

Methods.

The object of the studies being primarily to ascertain the bionomics of actual and potential vectors of malaria in the area, the principal study was concentrated on the anthropophilous species which feed in the vicinity of human habitations.

Two village areas were selected for observation. One, Kakuri, including four hamlets, is situated about two miles south of Kaduna and within a mile of the Kaduna river. The other, Kangimi, includes two hamlets, Kangimi and Sarkin Noma, which lie about 20 miles north of the capital and are in close proximity to small swampy streams.

The seasonal fluctuation of endophilous species was measured by visiting three or four huts in each hamlet at monthly intervals, making early-morning pyrethrum floor-sheet collections and calculating the Average Anopheles Densities (A.A.D.) per hut per day. Mosquitos collected in this way were dissected and the sporozoite rates recorded.

Trap catches.

The entrance and exit times of endophilous species were studied by using similar methods to those of Wharton (1951). In the present work, however, 'door traps' were used instead of window traps. The door trap consists of a large panel of plywood mounted on a frame which fits the doorway of the hut. In the centre of the panel is a baffle with a narrow horizontal slit as in a typical Magoon trap; above this is a square hole over which a gauze funnel trap can be fastened. With the slit open and the entrance of the funnel trap opening into the hut, the mosquitos are allowed to enter the hut, and many of those which attempt to leave are caught in the funnel trap. With the slit closed and the entrance of the funnel trap facing outwards, many mosquitos are caught as they attempt to enter the hut. Since in huts of this kind many mosquitos enter and leave by other routes, such traps cannot be used to estimate actual numbers, but if it be assumed that the proportion caught in traps is fairly constant between catching periods, then the activity rhythm of entry and exit can be ascertained.

The trapping experiments were carried out from July to October 1958.

Biting catches.

Seasonal fluctuations and biting times of anthropophilous mosquitos were studied by the regular use of human bait throughout the year. Since interest was centred on Anophelines, the biting catches were made only at night. Generally, four catchers were employed at any one time; they sat in total darkness and collected mosquitos in tubes as they were bitten, using their torches as sparingly as possible. Every hour the tubes of mosquitos were collected and labelled.

Three series of biting catches were made. (1) Short catches, lasting from 7.0 p.m. until 10.0 p.m., which were held about four times per month at one of the two regular catching stations in the bush. These stations were situated at about $\frac{1}{2}$ and $1\frac{1}{2}$ miles, respectively, from habitations; both were in close proximity to streams and marshy areas. These catches were made to ascertain the seasonal fluctuations in numbers of exophilous species. (2) All-night catches, from 8.0 p.m. until 6.0 a.m., both inside and outside a house, were held in the village of Kangimi from two to four times each month, between February and December 1958. This series of catches was made in order to obtain a clearer picture of

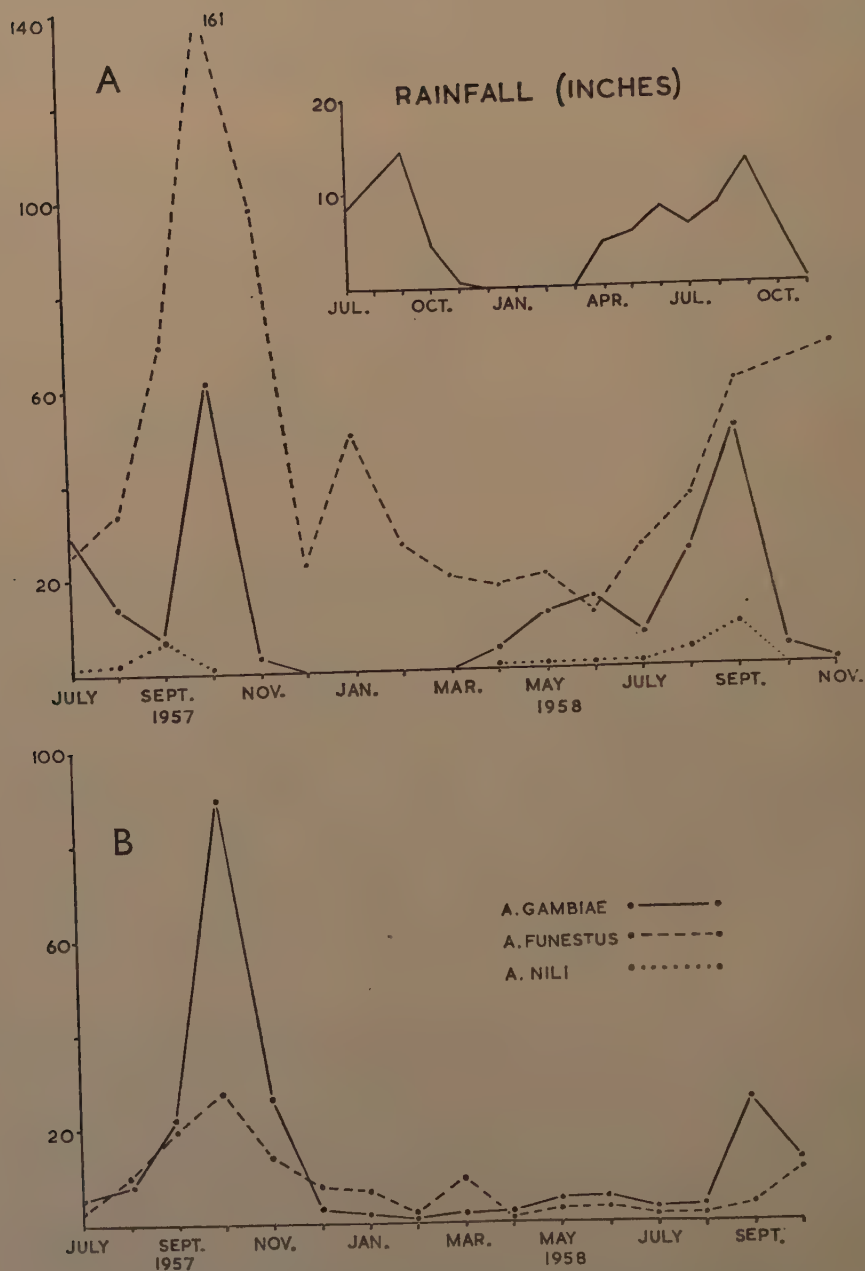


Fig. 1.—Average Anopheles Densities per room per day estimated from floor-sheet catches made between July 1957 and November 1958. A, northern district (Kangimi); B, southern district (Kakuri). Rainfall for the period is also shown.

the seasonal fluctuations of endophagous species than would be obtained by floor-sheet collections alone and at the same time to ascertain the reliability of the floor-sheet method in determining the numbers of mosquitos biting per night. The numbers of mosquitos taken outside and inside were later compared to find whether any preferences for outdoor or indoor feeding existed. (3) Short night catches were held in various localities merely to ascertain the distribution of species, all records made from this series are only included in the Appendix (p. 163).

Bionomics of the principal endophagous species of *Anopheles*.

The principal endophagous Anophelines of the area were *A. gambiae* Giles, *A. funestus* Giles, *A. nili* (Theo.) and *A. wellcomei* Theo. The first two species comprised almost the whole day-time resting populations obtained from huts by floor-sheet collections. It was not until the collection of mosquitos biting human bait was started that the possible importance of the other two species was realised.

Seasonal fluctuations.

The results of morning floor-sheet collections (Table II & fig. 1) show that, in the northern village area, *A. funestus* was the dominant species for all but two months of the year, its numbers being greatest at the end of the rains. In the southern area, *A. gambiae* predominated during the rains, whereas in the dry season both species occurred in similar low numbers. *A. nili* was found resting in huts only during the rains; it has never comprised more than 14 per cent. of the total Anopheline population of any hamlet.

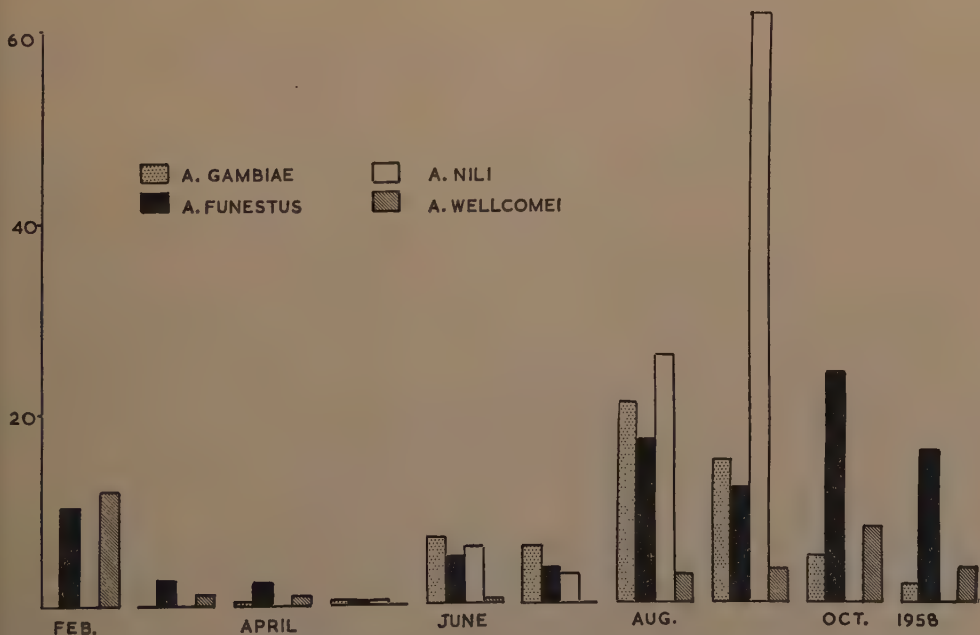


Fig. 2.—Seasonal fluctuations in numbers in endophagous species of *Anopheles* at Kangimi, Zaria Province. Data expressed as numbers caught biting at night per ten man-hours.

TABLE II.
Average Anopheles Densities.

Southern village area																
	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
<i>A. gambiae</i>	4	8	23	89	26	3	2	0.5	2	2.5	4.3	5	3	3	26	12
<i>A. funestus</i>	3	10	15	28	14	8	7	2	10	1	3	3	2	2	3.5	10
<i>A. nili</i>	0	2	0.5	1	0	0	0	0	0	0	0	0	0	1	1	0

Northern village area																
	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
<i>A. gambiae</i>	30	14	7	62	3	0	0	0	0	5	11	15	7	24	51	4
<i>A. funestus</i>	25	34	70	161	98	23	51	27	20	18	20	12	26	36	60	67
<i>A. nili</i>	0.5	2	8	1	0	0	0	0	0	0.1	0.5	0.5	0.1	4	9	0

In order to give a more complete picture of the fluctuations in numbers of the endophagous part of the mosquito population, the results of the all-night catches made in Kangimi hamlet are shown in fig. 2. It can be seen that *A. nili* and *A. wellcomei* are of greater importance than would appear from the results of the floor-sheet collections. *A. wellcomei* differed from the other three species in having a population peak at the height of the dry season. Unlike them, also, it was frequently taken from bush as well as from village stations (see fig. 6).

With a view to ascertaining the reliability of floor-sheet collections in determining numbers of endophagous mosquitos, an attempt is made in Table III to compare the numbers taken in floor-sheet collections in Kangimi hamlet with the numbers actually caught biting. Ideally, for such a comparison a large number of catching teams should have been employed in different huts but owing to the small staff only one could be used. Consequently a very close correlation between numbers caught biting in one hut and A.A.D.'s calculated from collections made in a number of huts cannot be expected. A further discrepancy is introduced since in the biting experiments the unit taken was the number of mosquitos caught biting one man in 10 hours whereas in actual fact the huts were normally only occupied for about 8 hours per night, thus one would expect rather more mosquitos recorded biting than in the floor-sheets. Before the two sets of figures can be compared it is necessary to divide the average numbers of freshly fed females in the floor-sheets by 2.5 (the average number of occupants).

From Table III it can be seen that only in *A. funestus* is there a reasonable correlation between the two sets of observations. Only in three of the ten monthly catches were the numbers recorded by one method more than double those recorded by the other. In *A. gambiae* the discrepancies between the two sets of observations are greater; in six of the eight months when the species was

TABLE III.

Comparison between A.A.D.'s calculated by floor-sheet collections and actual numbers of Anophelines caught biting one man per 10 hr.

	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.
No. man-hr. worked	40	50	40	20	40	80	80	40	40	28	40
No. nights	2	2	2	1	2	4	4	2	2	2	2
<i>A. gambiae</i>											
A.A.D. (total)	0	0	8	14	16	10	34	73	7	1	—
A.A.D. (fed)	0	0	6	7	9	7	22	60	6	1	—
No. fed per man	0	0	2.4	2.8	3.5	2.8	8.4	23.1	2.4	0	—
No. biting 1 man/10 hr. ..	0	0	0.2	0.2	7	6	21	15	5	2	0.2
<i>A. funestus</i>											
A.A.D. (total)	47	29	18	21	8	18	48	66	57	72	—
A.A.D. (fed)	17	8	14	10	3	8	32	41	37	46	—
No. fed per man	6.5	3.0	5.4	3.8	1.1	3.0	12.3	15.8	14.2	17.7	—
No. biting 1 man/10 hr. ..	10	3	2	0.2	5	4	17	12	24	16	6
<i>A. nili</i>											
A.A.D. (total)	0	0	0.3	1	1	0	7	15	0	0	—
A.A.D. (fed)	0	0	0.3	1	1	0	7	15	0	0	—
No. fed per man	0	0	0.1	0.4	0.4	0	2.7	5.8	0	0	—
No. biting 1 man/10 hr. ..	0	0	0	0.2	6	3	26	62	0.5	0	0
<i>A. wellcomei</i>											
No. biting 1 man/10 hr. ..	12	1	1	0	0.2	0	3	3.5	8	3.5	3

Note: No floor-sheet collections were made during December.

taken, numbers recorded by one method were over twice those made by the other but only in three months were the differences three times as great. In the case of *A. nili*, in all but two months, when numbers were very low, the numbers caught biting were far higher than those taken in the floor-sheets. The highest densities of *A. nili* recorded in floor-sheet collections were 15 per hut, i.e., 6 per man/hut, but the corresponding number actually caught biting one man per 10-hour night was over ten times this number. During August and September, *A. nili* was the dominant species biting indoors. *A. wellcomei* was never recorded in floor-sheet collections although it was caught biting in nine of the eleven months when observations were made. From these observations it does appear that whereas the floor-sheet method may be quite adequate for determining the numbers of *A. funestus* and perhaps *A. gambiae* biting at night, it is not so for *A. nili* or *A. wellcomei*. Of the total number of *A. nili* biting, only a very small proportion were found to remain in the huts at dawn, and of *A. wellcomei*, only two specimens have ever been recorded in floor-sheets by the writer. Should either of these species be incriminated as a vector of malaria, control by house spraying with residual insecticides would prove difficult, owing to their short stay in huts.

Sporozoite rates.

The proportion of *A. funestus* and of *A. gambiae* infected with malarial parasites was approximately the same, the dry-season sporozoite rates being half of those found during the wet season. No infection was found in any example of *A. nili* or *A. wellcomei* examined.

TABLE IV.

Sporozoite rates in principal species of *Anopheles* in Zaria Province.

Species	Period	No. dissected	No. positive	Rate (%)
<i>A. funestus</i>	Dec. 1957—May 1958	190	6	3
	June—Oct. 1958	334	26	7.7
<i>A. gambiae</i>	Nov. 1957—May 1958	100	4	4
	June—Oct. 1958	238	16	6.7
<i>A. nili</i>	Wet seasons 1957 and 1958	144	0	0
<i>A. wellcomei</i>	Whole period	68	0	0

Times of entry into and departure from houses.

Between July and October 1958, three huts at the observation hamlet of Kangimi were selected as trapping huts. Entrance door traps (see p. 147) were placed in position on six nights and exit traps on ten nights at intervals of at least a week. The traps were fastened at 9.0 p.m. and removed and replaced by empty traps at 11.0 p.m., 1.0 a.m., 3.0 a.m., 5.0 a.m. and 6.0 a.m. The mosquitos caught in the entrance traps (Table V) were practically all unfed, and no distinction is made in fig. 3, but those in the exit traps were at all stages of nourishment (Table VI) and therefore the numbers in each stage are shown separately in fig. 4.

The numbers caught in the entrance traps show that all three of the principal endophagous species, *A. gambiae*, *A. funestus* and *A. nili*, entered in greatest numbers between 9.0 and 11.0 p.m., i.e., before the occupants slept. *A. gambiae* in this area entered earlier than in French West Africa, where the maximum entry was recorded between 11.0 p.m. and 1.0 a.m. (Holstein, 1952). In this

TABLE V.

Numbers of Anophelines caught in 18 entrance traps.

Time of fixing	Time of removal	<i>A. gambiae</i>				<i>A. funestus</i>				<i>A. nili</i>			
		UF	FF	HG	G	UF	FF	HG	G	UF	FF	HG	G
9.0 p.m.	11.0 p.m.	32	0	0	0	22	0	0	0	19	1	0	0
11.0 p.m.	1.0 a.m.	7	1	0	0	5	0	1	0	2	0	0	0
1.0 a.m.	3.0 a.m.	2	0	0	0	8	0	0	0	13	0	0	0
3.0 a.m.	5.0 a.m.	0	0	0	0	5	0	1	0	1	0	0	0
5.0 a.m.	6.0 a.m.	7	0	2	0	3	1	3	1	3	1	0	0

UF—unfed; FF—fully fed; HG—half gravid; G—gravid.

species, two-thirds of the total caught in the Kangimi traps entered between 9.0 and 11.0 p.m. but in *A. funestus* and *A. nili* only one-half of the total entered early. At all times between 11.0 p.m. and dawn, *A. funestus* entered fairly regularly but *A. nili* showed a well marked second peak of entrance between 1.0 and 3.0 a.m.

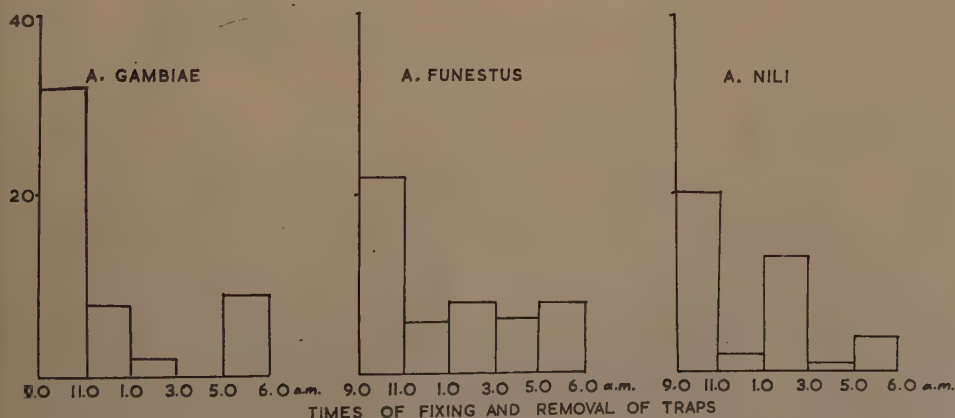


Fig. 3.—Entrance times of species of *Anopheles* into native huts. The figures are the totals of each species caught in three door traps used on six nights.

The catches from exit traps show that in all three species the maximum exodus occurred before 5.0 a.m., well before dawn. In *A. gambiae* and *A. funestus*, the peak occurred between 3.0 and 5.0 a.m. Of those caught leaving

between 1.0 and 5.0 a.m., 64 per cent. of *A. gambiae* and 63 per cent. of *A. funestus* were unfed, most of the remainder being gorged. A large proportion of the numbers of all three species caught leaving between 9.0 and 11.0 p.m. was also unfed. There was no well marked dawn exodus. In the case of *A. gambiae*,

TABLE VI.

Numbers of Anophelines caught in 30 exit traps.

Time of fixing	Time of removal	<i>A. gambiae</i>					<i>A. nili</i>					<i>A. funestus</i>				
		UF	FF	HG	G	Total	UF	FF	HG	G	Total	UF	FF	HG	G	Total
9.0 p.m.	11.0 p.m.	46	3	3	3	55	13	8	2	2	25	67	6	6	1	80
11.0 p.m.	1.0 a.m.	14	13	2	0	29	10	13	3	0	26	7	13	1	0	21
1.0 a.m.	3.0 a.m.	66	33	3	0	102	21	52	2	0	75	36	8	4	0	48
3.0 a.m.	5.0 a.m.	104	51	8	2	165	20	42	2	0	64	68	41	10	0	119
5.0 a.m.	6.0 a.m.	35	28	8	0	71	4	18	1	0	23	25	27	4	1	57
Total		265	128	24	5	422	68	133	10	2	213	203	95	25	2	325

only 16.8 per cent. of the total number caught in the exit traps left between 5.0 and 6.0 a.m., in *A. funestus* 17.6 per cent. and in *A. nili* 10.8 per cent.

The behaviour of *A. nili* differs from that of the other two species mainly in the fact that only 30 per cent. of those leaving between 1.0 and 5.0 a.m. were unfed.

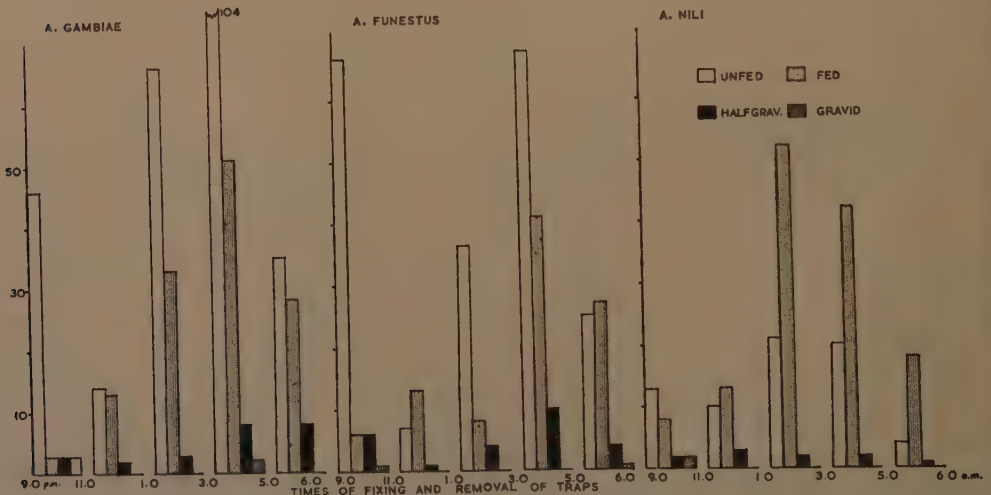


Fig. 4.—Times of exit of species of *Anopheles* from native huts. The figures are the total numbers of each species caught in three door traps used on ten nights.

Times of feeding inside houses.

The biting times for the different endophagous species were recorded in the same hut and by the same personnel but on different occasions. The records included in Table VII and fig. 5 comprise catches made on nights when the

species concerned occurred frequently. To obviate discrepancies due to weather inhibiting biting, catches were only recorded on nights when mosquitos were biting continuously. During this series of catches only two catchers operated at a time so twice as many man-hours were worked as there were nights. Since

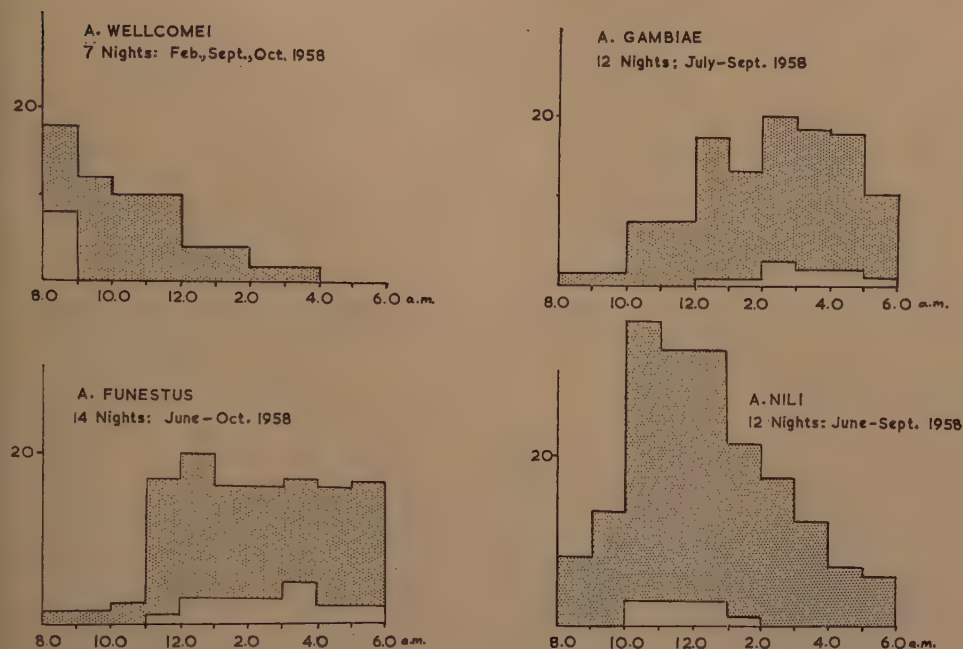


Fig. 5.—Biting times of endophagous species of *Anopheles*. Data expressed as numbers of each species biting ten men per hour (stippled) and as the numbers of nights when majority were caught at a given time (clear).

records for the various species were sometimes made over a different number of nights, to facilitate comparison of the results the catches in each period are shown as the numbers biting 10 men per hour at that period, abbreviated to "No. per 10 man-hr." in Table VII.

A. wellcomei.—Maximum biting activity was recorded between dusk and 9.0 p.m., gradually falling off until 4.0 a.m., when activity ceased.

A. gambiae.—Small numbers were caught biting from 8.0 p.m. but activity was greatest between 2.0 a.m. and 5.0 a.m. This behaviour differs from that of an exophilous population of *A. gambiae* studied in forest country at Itowolo, near Lagos (Mattingly, 1949), and at Bwamba, Uganda (Haddow, Gillett & Highton, 1947). In these localities the peak was found to be during the period of nautical twilight (sun 6° – 12° below the horizon).

A. funestus.—This species came to bait very regularly throughout the night from 11.0 p.m. until dawn.

A. nili.—Biting commenced at 8.0 p.m., rising to a definite peak between 10.0 p.m. and 1.0 a.m. then falling gradually until dawn.

Preferences for indoor and outdoor feeding.

In order to determine whether species regarded as endophagous do in fact prefer to feed inside a hut when other food is available outside, a series of 18

TABLE VII.
Biting times of the principal anthropophilous species of *Anopheles*.

Period	<i>A. gambiae</i> (12 nights, 24 man-hr.)		<i>A. funestus</i> (14 nights, 28 man-hr.)		<i>A. nili</i> (12 nights, 24 man-hr.)		<i>A. wellcomei</i> (7 nights, 14 man-hr.)	
	Total caught	No. per 10 man-hr.	Total caught	No. per 10 man-hr.	Total caught	No. per 10 man-hr.	Total caught	No. per 10 man-hr.
8.0—9.0 p.m.	4	1.7	4	1.4	19	8.0	25	18.0
9.0—10.0 p.m.	3	1.3	5	1.8	33	13.8	17	12.0
10.0—11.0 p.m.	18	7.5	7	2.5	87	36.2	13	9.3
11.0 p.m.—midnight	19	7.8	49	17.5	78	32.5	13	9.3
midnight—1.0 a.m.	42	17.5	55	20.0	79	32.9	6	4.3
1.0—2.0 a.m.	32	13.3	46	16.4	52	21.7	5	3.6
2.0—3.0 a.m.	47	20.0	43	15.4	42	17.5	3	2.2
3.0—4.0 a.m.	45	18.7	50	17.8	30	12.5	2	1.4
4.0—5.0 a.m.	43	18.0	45	16.0	17	7.0	0	0
5.0—6.0 a.m.	26	10.8	47	16.8	15	6.5	0	0

night catches was made between February and October 1958. One catching team of two men worked inside a hut, another about ten yards away, outside, the personnel being changed every hour. It should be mentioned here that the catches made by the team inside the hut were also used to calculate the biting activity times recorded in the preceding study.

TABLE VIII.

Numbers of Anophelines biting human bait outdoors and indoors.

Date	<i>A. wellcomei</i>		<i>A. nili</i>		<i>A. gambiae</i>		<i>A. funestus</i>	
	Out	In	Out	In	Out	In	Out	In
3/2	14	22	0	0	0	0	0	0
12/2	26	13	0	0	0	0	6	34
20/2	14	3	0	0	0	0	1	2
28/2	25	9	0	0	0	0	1	6
23/4	0	2	1	0	0	0	0	3
23/5	1	0	7	2	4	2	1	2
25/6	1	0	14	21	5	15	1	14
2/7	0	0	14	2	35	9	6	5
10/7	0	0	11	4	33	9	10	9
17/7	0	0	10	7	27	21	5	9
24/7	0	0	26	7	10	14	0	2
31/7	0	0	5	3	24	4	13	7
8/8	0	0	62	24	25	13	5	15
15/8	0	0	16	12	24	25	8	28
22/8	0	0	40	51	135	43	26	39
28/8	20	26	87	118	171	86	16	56
11/9	5	5	99	70	67	37	33	33
23/10	2	3	0	0	8	5	27	25

Dry season, four catches in February; wet season, 14 catches between April and October.

Summary of Table VIII.

	<i>A. wellcomei</i>		<i>A. nili</i>		<i>A. gambiae</i>		<i>A. funestus</i>	
	Out	In	Out	In	Out	In	Out	In
Dry season								
No. of nights on which species was taken	4	4	0	0	0	0	3	3
No. caught (dry season) ..	79	47	0	0	0	0	8	42
No. of nights when majority taken out or indoors ..	3	1	0	0	0	0	0	2
Wet season								
No. of nights on which species was taken	5	4	13	12	13	13	12	14
No. caught (wet season) ..	29	36	392	321	568	283	151	247
No. of nights when majority taken out or indoors ..	0	2	9	3	10	2	2	8

Note: A majority is only recorded when the difference between numbers taken inside and outside is more than one.

The results (Table VIII) show that, in the wet season, over twice as many examples of *A. gambiae* were caught outside as inside, of *A. funestus* the majority were caught inside, of *A. nili*, the majority outside. *A. wellcomei* was captured in about equal numbers inside and out, but numbers taken were small. In the dry season, *A. funestus* was even more endophagous, five times as many being caught inside as out. In the case of *A. wellcomei*, almost twice as many were taken outside as in. Here again, numbers were comparatively small, although the species appeared to be more abundant in the dry season than in the wet, and was then taken more frequently than any of the other three species. The species arranged in order of degree of endophagy over the whole year are—*A. funestus* 64.5 per cent. endophagous, *A. nili* 45 per cent., *A. wellcomei* 43.5 per cent., and *A. gambiae* 33.3 per cent.

Seasonal fluctuations in numbers of other prevalent species of *Anopheles*.

Apart from very infrequent specimens, no species of *Anopheles* other than those already discussed was taken biting or resting in huts. Excluding *A. wellcomei*, which has been considered earlier (pp. 149–158), six species of *Anopheles* were prevalent biting outdoors at some distance from human habitations. The seasonal fluctuations in numbers of these exophagous species in Zaria Province was estimated from numbers caught outdoors at human bait during the short night catches held at bush stations (p. 147). All of them showed some seasonal fluctuation in numbers (fig. 6), the majority being more abundant during the

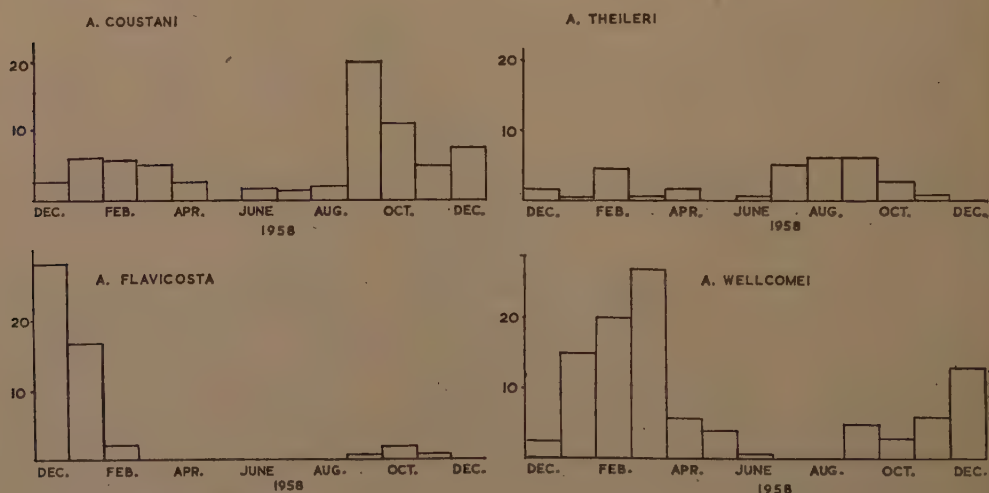


Fig. 6.—Seasonal fluctuations in numbers of three purely exophagous species of *Anopheles*. Data expressed as the numbers caught biting at night per ten man-hr. at bush stations. The histogram for *A. wellcomei* taken at these stations is also included (see p. 151).

rains, populations reaching a peak towards the end. This peak was less marked in *A. coustani* Lav. and *A. theileri* Edw., which occurred in moderate numbers throughout the year. *A. squamosus* Theo. and *A. rufipes* (Gough) were absent from catches during the first half of the rains, whilst *A. pharoensis* Theo. was only taken at the end of the wet season. One species, *A. flavicosta* Edw., was most frequently recorded at human bait in the middle of the dry season.

Biting times could only be observed in the case of two of these exophagous species, *A. coustani* and *A. theileri*, which were commonly taken biting at Kangimi hamlet, because all-night catches were not held at the bush stations.

where the other species were prevalent. *A. coustani* was taken at all hours of the night. *A. theileri* was frequent between 8.0 p.m. and 2.0 a.m. In both species the peak of biting was before 9.0 p.m. (fig. 7).

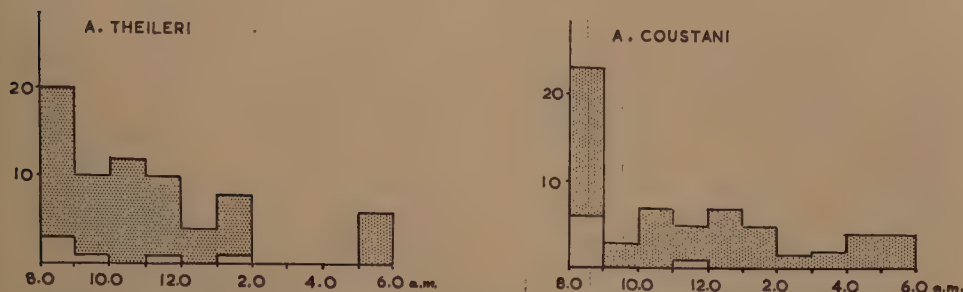


Fig. 7.—Biting times of two purely exophagous species of *Anopheles*. Data from village catches expressed as numbers of each species biting ten men per hour (stippled) and as the number of nights when majority were caught at a given time (clear).

Seasonal fluctuations in numbers of the principal nocturnal anthropophilous species of Culicinae.

The seasonal fluctuations of nocturnal anthropophilous species of the CULICINAE was studied from the various biting catches (see p. 147) held regularly between December 1957 and November 1958. Only very few Culicines were taken indoors, so all records below refer to exophagous species. Since the catches were made in

TABLE IX.

Seasonal fluctuations in numbers of some species of CULICINAE caught outdoors at human bait during the hours of darkness.

Month	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.
No. of man-hours worked	25	39	49	22	20	26	37	71	70	71	43	37
Species	Numbers of mosquitos caught biting per 10 man-hours											
<i>Mansonia africana</i>	2	0.2	0.2	0.5	2	0	0.5	0.3	0.4	1	32	4
<i>M. uniformis</i> ..	38	11	4	5	9	14	12	9	8	11	62	24
<i>M. cristata</i>	0	0.5	1	0.5	0.5	0	0	0.1	0	0	0.4	0
<i>Aedes lineatopennis</i>	1.6	0	0	0	6.5	1.5	1	0.3	0.1	3.4	64	1
<i>Culex poicilipes</i> ..	0	2	2	4	1	0	0	0	0	0	0	1
Rainfall (in.) ..	0	0	0	0	4	5	8	6	8	13	8	0

rural areas, no records were obtained of *Culex pipiens fatigans* Wied., the most important nuisance mosquito of the towns. Similarly, since the catches were

made at night, insufficient information was obtained on the fluctuations of persistent day-time biters such as *Aedes argenteopunctatus* (Theo.). The data for the five species that occurred most frequently are shown in Table IX, and for four of them also in fig. 8.

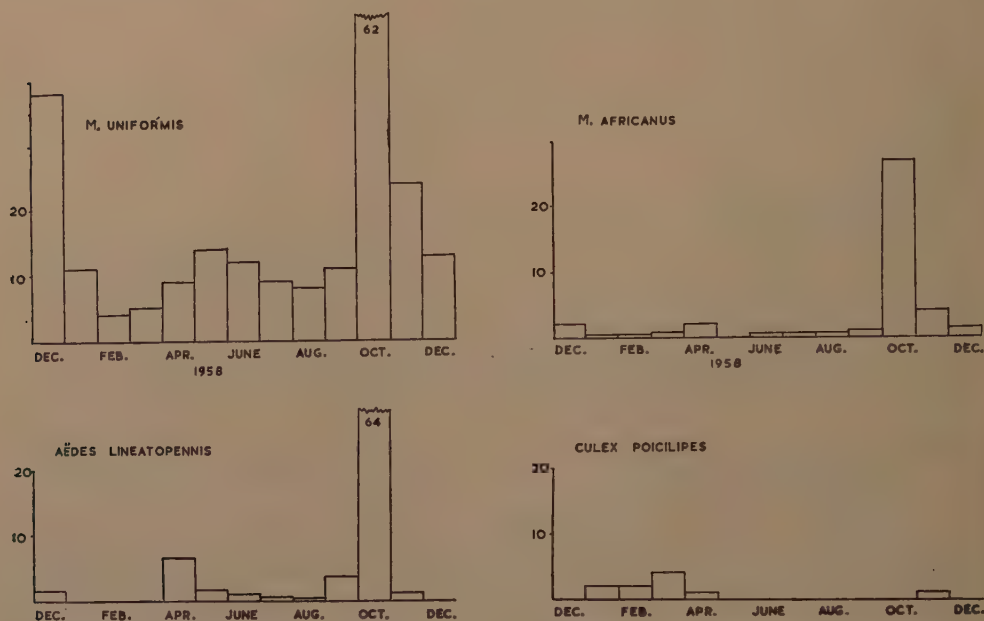


Fig. 8.—Biting times of exophagous species of Culicines. Data expressed as numbers of each species biting ten men per hour.

Discussion.

Comparison of the Average Anopheles Densities of the four principal species of *Anopheles* calculated by floor-sheet collections and actual numbers biting (Table III) show that *A. nili* was largely exophilous and *A. wellcomei* completely so whilst the individuals of both *A. gambiae* and *A. funestus* that bit indoors were mainly endophilous. By using nocturnal catching teams (Table VIII) it was found that *A. gambiae* definitely preferred to feed outside, twice as many specimens being caught outside as inside. It must be pointed out, however, that *A. gambiae* cannot be regarded as normally exophagous in the area since the human host is indoors at the period of maximum feeding. If it were naturally exophagous, one would expect to find large numbers in outdoor resting places, but this is not the case; only very few specimens have been found resting in holes in banks or under culverts. A large number were, however, found resting under the eaves of huts: during September 1957, the eaves of six huts were sprayed with pyrethrum and this was followed by a floor-sheet collection inside the huts. In the case of *A. gambiae*, 10 per cent., and of *A. funestus*, 12 per cent., of the total was found in the eaves of thatched huts. *A. nili* also preferred to feed outdoors, but to a lesser degree than *A. gambiae*, whilst *A. funestus* preferred feeding inside. The numbers of *A. wellcomei* taken were too small for any definite conclusions to be drawn but they suggest that there may be seasonal differences in behaviour pattern, and this may possibly be true in other species also. Although *A. nili* and *A. wellcomei* have never been found infected with sporozoites in the area, their study is considered to be necessary since in French

West Africa *A. nili* has a sporozoite rate of 4.0 and *A. wellcomei* 0.01 per cent. (Hamon, Adam & Grjebine, 1956).

The door-trap and biting catches showed that a marked entrance peak of unfed examples of *A. gambiae*, *A. funestus* and *A. nili* occurred before 11.0 p.m. In the case of *A. gambiae* the maximum period of biting may be taken as either between 2.0 and 5.0 a.m., or, if the subsidiary peak between midnight and 1.0 a.m. is included, between midnight and 5.0 a.m. Thus, there is a delay of at least one hour between time of entering and start of maximum biting, even in the unlikely event of all the specimens caught in the 9.0–11.0 p.m. trap entering at 11.0 p.m. It would probably be more accurate if the mid-point of the time of entry were taken, in which case the delay would be two hours. This agrees with the findings of Halerow (1956). In the case of *A. funestus*, where the time of onset of maximum biting was 11.0 p.m., there was one hour less interval than occurred with *A. gambiae*. The position with regard to *A. nili* was complicated by the second entrance peak which occurred between 1.0 and 3.0 a.m., but the first entrance peak apparently coincided with the commencement of the peak biting period, so delay, if any, is very slight. The above comments on the apparent delay between times of entrance and onset of feeding can only be very tentative, since a rather different picture would be given if the peak of biting were taken as the hour in which the majority of mosquitos bit most frequently (fig. 6, clear blocks in histogram).

The most surprising phenomenon brought to light by the trapping experiments was the very high proportion of unfed mosquitos amongst those caught leaving the huts. In the case of both *A. gambiae* and *A. funestus*, almost two-thirds of those leaving between 1.0 and 5.0 a.m. were unfed, but less than one-third only of the total of *A. nili* leaving between those times were unfed. The only explanation the writer can suggest is that *A. nili* is a more persistent biter than the other two species, but there is no real evidence to support this supposition.

Summary.

A general survey of the species of *Anopheles* in Zaria Province, Northern Nigeria, carried out between June 1957 and December 1958, was designed primarily to ascertain the bionomics of actual and potential vectors of malaria there. The studies, which were centred upon the four principal domestic Anophelines, *A. gambiae* Giles, *A. funestus* Giles, *A. nili* (Theo.) and *A. wellcomei* Theo., were carried out by making regular floor-sheet collections and entrance- and exit-trap catches in native huts, together with biting catches inside and outside huts. Data on other Anophelines and Culicines, taken at the same time, were also recorded.

The studies show that in this region, where malaria is holoendemic, all four species are endophagous to a greater or lesser extent although both *A. gambiae* and *A. nili* prefer to feed outside if a host is available. Only two species have been incriminated as vectors, *A. gambiae*, which had a sporozoite rate of between 4 and 7 per cent., and *A. funestus* with between 3 and 8 per cent., according to the season.

Collections by floor-sheets and by catches at human bait showed that *A. gambiae*, *A. funestus* and *A. nili* were predominantly wet-season species, although in one village area studied *A. funestus* also occurred in fairly high numbers throughout the dry season. *A. wellcomei*, on the other hand, was shown to be a predominantly dry-season species.

By using traps and making collections with human bait, the entrance, exit and biting times of *A. gambiae*, *A. funestus* and *A. nili* were ascertained. The largest numbers of *A. gambiae* and *A. funestus* entered huts between 9.0 and 11.0 p.m. and left between 3.0 and 5.0 a.m., the maximum biting activity for *A. gambiae* being between midnight and 5.0 a.m., and for *A. funestus* between

11.0 p.m. and dawn. *A. nili* differed considerably from the other two species, having two peaks of maximum entry, between 9.0 and 11.0 p.m. and 1.0 and 3.0 a.m., the period of maximum exodus being between 1.0 and 5.0 a.m., with a peak of biting activity between 10.0 p.m. and 1.0 a.m. It was found that a very high proportion of the mosquitos caught leaving the huts was unfed; between 1.0 and 5.0 a.m., 64 per cent. of *A. gambiae* leaving, 63 per cent. of *A. funestus* and 30 per cent. of *A. nili* were unfed.

Apart from the four domestic species of *Anopheles* mentioned above, the only other anthropophilous species which could be described as common in the vicinity of Kaduna were *A. coustani* Lav., *A. theileri* Edw., *A. flavicosta* Edw. and *A. rufipes* (Gough). *A. implexus* (Theo.) is recorded from Nigeria for the first time.

The commonest species of Culicines taken at human bait during outside night collections were *Mansonia africana* (Theo.), *M. uniformis* (Theo.), *M. cristata* (Theo.), *Aedes lineatopennis* (Ludl.) and *Culex poicilipes* (Theo.). Of these, *M. uniformis* was by far the most regular and persistent biter throughout the year. *M. africana*, on the other hand, was only taken in any numbers during October.

In an appendix, a list of 17 species of *Anopheles* (including 3 varieties), 65 of the CULICINAE and two of the TOXORHYNCHITINAE known to occur in Zaria Province is given, with notes on their distribution and bionomics.

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References.

- ADAM, J. P., HAMON, J., RICKENBACH, A. & LIPS, M. (1957). I. Description du mâle et du pharynx de la femelle d'*Anopheles brohieri* Edwards 1929 et *A. hancocki* var. *masseguini* Hamon 1954. II. Étude des affinités existant entre *Anopheles hancocki*, *A. hancocki* var. *masseguini*, *A. brohieri*, *A. theileri*, *A. seydeli*.—*Bull. Soc. Path. exot.* **49** (1956) pp. 747-758.
- HADDOW, A. J., GILLET, J. D. & HIGHTON, R. B. (1947). The mosquitoes of Bwamba County, Uganda. V.—*Bull. ent. Res.* **37** pp. 301-330.
- HALCROW, J. G. (1956). Ecology of *Anopheles gambiae* Giles.—*Nature, Lond.* **177** pp. 1103-1105.
- HAMON, J., ADAM, J. P. & GRJEBINE, A. (1956). Observations sur la répartition et le comportement des Anophèles de l'Afrique-Equatoriale Française, du Cameroun et de l'Afrique Occidentale.—*Bull. World Hlth Org.* **15** pp. 549-591.
- HANNEY, P. W. (1959). Variation in *Anopheles flavicosta* Edwards from Northern Nigeria.—*Proc. R. ent. Soc. Lond. (B)* **28** pp. 169-174.
- HANNEY, P. W. [1960]. Notes on the distribution of *Aedes aegypti* Linnaeus in Zaria Province, Northern Nigeria.—*Entomologist* **92** pp. 250-253.

- HOLSTEIN, M. H. (1952). *Biologie d'Anopheles gambiae*. Recherches en Afrique-Occidentale Française.—*Monogr. Ser. World Hlth Org.* no. 9, 176 pp.
- MATTINGLY, P. F. (1944). New keys to the West African Anophelini.—*Ann. trop. Med. Parasit.* **38** pp. 189–200.
- MATTINGLY, P. F. (1947). Notes on the early stages of certain Ethiopian mosquitoes, with some locality records from British West Africa.—*Ann. trop. Med. Parasit.* **41** pp. 239–252.
- MATTINGLY, P. F. (1949). Studies on West African forest mosquitos. Part I. The seasonal distribution, biting cycle and vertical distribution of four of the principal species.—*Bull. ent. Res.* **40** pp. 149–168.
- PETERS, W. (1956). The mosquitos of Liberia (Diptera: Culicidae), a general survey.—*Bull. ent. Res.* **47** pp. 525–551.
- WHARTON, R. H. (1951). The habits of adult mosquitoes in Malaya. I–II.—*Ann. trop. Med. Parasit.* **45** pp. 141–160.

APPENDIX.

A list of all species of ANOPHELINAE, CULICINAE and TOXORHYNCHITINAE recorded from Zaria Province, with notes on their distribution and bionomics.

***Anopheles coustani* Lav. and *A. coustani* var. *ziemanni* Grünb.**

Both the type form and var. *ziemanni* are common in the area. They are easily distinguishable from each other as no intermediates have been found. In the type form, the white markings at the base and apex of the first hind tarsal segment and at the apex of the second segment are always twice the size of the corresponding bands in var. *ziemanni*. There appears to be a seasonal alternation in numbers in at least some localities. During short night catches made in the Kaduna area during the wet season, 66 examples of *A. coustani sensu lato* were caught, of which 11 were var. *ziemanni*; during the dry season 65 were caught, of which 58 were var. *ziemanni*.

In many examples of *A. coustani typicus* the black ring at the base of the third hind tarsal segment was absent. Fed specimens of both types were commonly captured in goat stables and in traps baited with sheep, donkey and goat. *A. coustani* was taken outdoors at human bait at all hours of the night, the peak being before 9.0 p.m. (fig. 7). A few specimens have been caught biting indoors. Larvae of both forms were common in overgrown streams.

***A. implexus* (Theo.).**

This species is confined to isolated belts of gallery forest bordering streams. It was quite abundant during both the wet and dry seasons and was a most persistent biter. During surveys it was observed to bite at all times between 12.0 noon and 9.0 p.m. Larvae were frequent in small temporary pools in the forests. Since the areas where it occurs are rarely visited by humans, *A. implexus* must be largely zoophilous. It has not previously been recorded from Nigeria, but its occurrence in the Northern Region was predicted by Mattingly (1944).

***A. nill* (Theo.).**

A common wet-season species. Fed specimens sometimes found resting in sheds occupied by horse, goat or pig. The seasonal fluctuation in numbers and the biting and resting behaviour of the adults have already been discussed in detail (pp. 149–158).

A. brunnipes (Theo.).

A single specimen was caught biting outdoors at midnight in December 1957.

A. longipalpis var. **domicolus** Edw.

Only three females were captured during the 18-month period; from a goat stable (Aug. 1957), from an undercut bank (Aug. 1957) and one caught biting outdoors at midnight during December 1957.

A. funestus Giles.

Only larvae of the type form have been found by the writer. This species appears to be almost totally anthropophilous. In one observation village, huts were found which sheltered both man and goat; of 56 bloods from examples of *A. funestus* taken in such huts, all were positive only for man. The seasonal fluctuation in numbers and the biting and resting behaviour of the adults have already been discussed in detail (pp. 149-158).

A. flavicosta Edw.

A common outdoor biter during the dry season. Several fed specimens have been taken from traps containing sheep and goat, also from horse stables. Bloods taken from specimens found resting in poultry houses were found to be positive for avian blood. Larvae have only been obtained from one swamp by trampling the tall grass and collecting from the puddles formed. Examination of larvae and associated adults has led the writer to conclude that all previous records of *A. moucheti* Evans made in this area refer to *A. flavicosta* (Hanney, 1959).

A. hancocki Edw.

Two females were taken resting in goat stables in August 1957. Three were caught biting human bait between 5.0 and 6.0 a.m. in September 1958, one being taken indoors. Recorded by Brown as breeding in small streams near Kaduna.

A. lesoni Evans.

Recorded from Kaduna by Brown in 1942 (Malaria Service records).

A. theileri Edw. and **A. theileri** var. **septentrionalis** * Evans.

Both the typical form and var. *septentrionalis* were most abundant during the rains (fig. 6), frequently being caught outdoors at human bait between 8.0 p.m. and 2.0 a.m., the peak of biting being before 9.0 p.m. (fig. 7). The two keep fairly separate from one another. In the northern observation area the numbers caught during the period were 115 of *A. theileri* and 20 of var. *septentrionalis*. In the Kaduna southern area the numbers were 2 of *A. theileri* and 20 of var. *septentrionalis*. Several specimens have been obtained in traps baited with goat and sheep and occasionally biting in houses. The larvae have been found in stagnant ditches with profuse emergent vegetation.

A. wellcomei Theo.

Larvae have only been found amongst floating vegetation in small open pools in a watercourse. The seasonal fluctuations in numbers and the biting and resting behaviour of the adults have already been discussed in detail (pp. 149-158).

* Considered by Adam, Hamon, Rickenbach & Lips (1957) to be a synonym of *A. hancocki brohieri* Edw.—Ed.

A. gambiae Giles.

During the wet season, many adults of *A. gambiae* and also of *A. funestus* were found infested with nematodes (*Agamomermis*). In many cases the nematodes so filled the haemocoel that the ovaries could not develop. Of 48 examples of *A. gambiae* examined, 2 (4%) were infested; in 107 of *A. funestus* examined 10 (9%) were infested. The writer is of the opinion that transmission may be through hydrachnid mites with which a number of adult mosquitos were found to be infested. Of 178 adults of *A. gambiae* examined, 32 (18%) carried mites. The seasonal fluctuations in numbers and the biting and resting behaviour of the adults have already been discussed in detail (pp. 149-158).

A. maculipalpis (Giles).

A few specimens have been caught biting outdoors during the wet season. Fed females have also been captured resting in goat stables. Larvae were occasionally found in shallow swamps and cocoa yam plantations.

A. pretoriensis (Theo.).

This species has never been taken at bait and only very few recorded as resting in houses. Very few breeding sites were found during the survey but in those it was abundant. It appears to prefer clear water without vegetation and a slight flow, as in irrigation furrows.

A. rufipes (Gough).

Both the type form and var. *ingrami* Edw. were taken outdoors at human bait at the end of the rains. The larvae, however, were amongst the most common species at all times of the year, chiefly in exposed streams and small marshy pools. *A. rufipes* was only occasionally found resting in huts but was quite frequent in stables occupied by goat or horse and appears to be mainly zoophilous.

A. pharoensis Theo.

Very small numbers were captured outdoors at human bait towards the end of the rains. In 672 huts examined during the survey, only one example of *A. pharoensis* was found resting indoors.

A. squamosus Theo.

Small numbers of this species have been taken outdoors at human bait throughout the dry season, the peak being at the end of the rains. It appears to be primarily exophilous but has been found rarely in goat stables. Breeding places included streams, hoof prints and shallow swamps.

Harpagomyia taeniarostris Theo.

A single larva was found in a banana axil, July 1958. The plant was situated on the edge of a fringing forest.

Uranotaenia alboabdominalis Theo.

Adults were commonly found resting in crab-holes. One specimen was caught in a trap baited with sheep. Larvae were quite common in ground pools in fringing forest.

U. bilineata var. *connali* Edw.

This form was found only in the fringing forests. Small numbers of adults were captured during the wet season but in the dry season, when the water level in the forest had risen considerably owing to increased flow from springs, large numbers were found resting on the surface of leaf-covered pools.

U. chorleyi Edw.

Larvae were found in a small pool in a forest stream-bed during April 1958.

U. annulata Theo.

A very common species breeding in crab-holes throughout the year.

U. ornata Theo.

Larvae were commonly found in the axils of banana plants growing in the shade of fringing forest.

U. mashonaensis Theo.

The only breeding places recorded were small pools in forest streams. These pools were full of dead leaves and with a pH 5.6.

Aëdomyia africana Nev.-Lem.

A single female was bred from larvae obtained from a *Pistia*-covered borrow pit in Zaria City.

Ficalbia (Mimomyia) splendens (Theo.).

Regularly found breeding in *Pistia*-covered borrow pits.

F. (M.) hispida (Theo.).

Adults were obtained by sweeping tall grass in a swamp at Kaduna during February and July 1958.

F. (M.) flavopicta Edw.

A single female was found resting in September 1958 under a tree trunk in a narrow belt of forest.

F. (M.) mimomyiaformis (Newst.).

A single specimen was bred from larvae taken from borrow pits in Zaria in June 1958.

F. (M.) plumosa (Theo.).

Larvae have occasionally been found in seasonally flooded depressions and pools in the Kaduna area.

Mansonia (Coquilleltidia) maculipennis (Theo.).

Adults were frequently found resting amongst foliage in belts of fringing forest.

M. (C.) cristata (Theo.).

Adults were regularly caught outdoors in the dry season at human bait. Specimens have been caught biting inside houses.

M. (Mansonioides) africana (Theo.).

Small numbers were caught at human bait throughout the year but large numbers were only recorded at the end of the rains (fig. 8).

M. (M.) uniformis (Theo.).

A vicious outdoor biter throughout the year, its numbers being highest between October and December (fig. 8). It was frequently caught feeding in houses, also in traps baited with sheep and donkey.

Aedes (Mucidus) mucidus (Karsch).

A single female was caught biting the writer outdoors at 8.30 p.m. in September 1958.

A. (Finlaya) longipalpis (Grünb.).

Larvae were once found in a pool in fringing forest in August 1957 (W. A. MacDonald, personal communication).

A. (F.) ingrami Edw.

A single female was bred from larvae obtained from a tree hole in fringing forest during August 1958.

A. (Stegomyia) aegypti (L.).

Larvae were frequently found in domestic utensils and in tree holes, both in villages and in sites three miles from human habitations. Twenty-five per cent. of pots which contained mosquito larvae of any kind were found to contain those of *A. aegypti*, irrespective of their distance from houses. In the case of tree holes, 54 per cent. of those near villages but only 20 per cent. of those situated three miles from habitations contained *A. aegypti*. *A. aegypti* ssp. *formosus* (Wlk.) was found in two-thirds of the total breeding places occupied by *A. aegypti*, *A. aegypti typicus* in the remainder. Two specimens of var. *queenslandensis* (Theo.) were bred from material collected from tree holes. *A. aegypti* was never taken at human bait in spite of the large number of collections made. It was also only rarely found resting in huts; eleven specimens were taken from a total of 672 huts sprayed with pyrethrum during the survey.

Further details of the distribution of this species are given in Hanney (1960).

A. (S.) simpsoni (Theo.).

Larvae were only found in banana axils.

A. (S.) apicoargenteus (Theo.).

A single female was bred from a tree hole in fringing forest.

A. (S.) africanus (Theo.).

A very common tree-hole breeder, particularly in fringing forest. Specimens were often caught biting at dusk.

A. (S.) luteocephalus (Newst.).

A common tree-hole breeder. Large numbers were caught biting at dusk during the early rains.

A. (S.) unilineatus (Theo.).

Larvae were obtained from three tree holes in the Kaduna area during 1958.

A. (S.) vittatus (Big.).

Larvae were very abundant in rock pools and in fallen concrete telegraph posts. Small numbers were often caught biting man during early evening in the

wet season. The species has never been found resting in houses but was quite common in goat stables. Blood taken from specimens resting in the latter was found by precipitin tests to be positive for goat.

A. (*Aëdimorphus*) *stokesi* Evans.

This was one of the commonest tree-hole breeding species.

A. (*A.*) *argenteopunctatus* (Theo.).

Larvae were once found in a small overgrown stream (pH 5.6) during July 1958. Adults were commonly caught at human bait during the early hours of darkness between July and December 1958. In November and early December this species was very troublesome in some localities during the afternoon when swarms of about a dozen would attack persistently.

A. (*A.*) *tarsalis* (Newst.).

Larvae were commonly found during the wet season in small pools in forest stream-beds. Breeding also took place in clay pots left in the forest and on one occasion a male was bred from a banana axil.

A. (*A.*) *minutus* (Theo.).

Adults were commonly caught at human bait, some fed specimens were also captured in a trap baited with sheep. Larvae have once been found in a pot left in a forest.

A. (*A.*) *dalzieli* (Theo.).

This species was frequently caught biting outdoors during the early hours of darkness in the wet season and more rarely in huts.

A. (*A.*) *cumminsi* ssp. *mediopunctatus* (Theo.).

Two females were caught biting man at 5.0 a.m. in July 1958.

A. (*A.*) *centropunctatus* (Theo.).

Only two records have been made for this species. A female was caught biting man at 9.0 p.m. in July and a larva was obtained from a crab-hole in January 1958.

A. (*A.*) *hirsutus* (Theo.).

A few specimens were caught biting outdoors during April, July and August 1958.

A. (*A.*) *fowleri* (Charmoy).

Larvae were found in a rock pool in May 1958. Adults were occasionally recorded biting at night during April and September.

A. (*Neomelaniconion*) *lineatopennis* (Ludl.).

Small numbers were regularly caught biting outdoors at all hours of the night excepting at the height of the dry season (fig. 8). Very high numbers (64 per 10 man-hours) were recorded biting in October 1958. During this month large swarms would often attack man during the afternoons.

A. (*N.*) *palpalis* (Newst.).

A few adults were found between July and September 1958 resting in damp situations in a narrow fringing forest. A single specimen was captured biting

the writer at 8.0 p.m. during August. Larvae have been recorded from a ground pool in the forest in 1957 (W. A. MacDonald, personal communication).

A. (*Diceromyia*) *furcifer* (Edw.).

Small numbers of adults were regularly taken biting man at night between April and October. Larvae recorded from pools in fringing forest.

A. (D.) *taylori* Edw.

Adults were bred from larvae collected from three tree holes.

***Eretmapodites chrysogaster* Grah.**

Profuse breeding was found in the 'nut shells' of *Landolphia*, husks of the fan palm (*Borassus aethiopum*) and in calabashes and gourds. All breeding places were in the vicinity of belts of forest.

E. *dracaenae* Edw.

A single male was bred from material collected in banana axils, the plants growing near fringing forest.

***Culex* (*Lutzia*) *tigripes* Grp.**

Larvae were very common in domestic utensils and in ground pools, frequently in foul water.

C. (*Neoculex*) *insignis* (Cart.).

Larvae were found in crab-holes throughout the year.

C. (N.) *wigglesworthi* Edw.

Breeding was recorded in tree holes and in pots left in a forest.

C. (N.) *horridus* Edw.

This was one of the commonest tree-hole breeding species found in the area.

C. (*Culiciomyia*) *nebulosus* Theo.

Larvae were frequent in domestic utensils and tree holes, often in dark-brown water.

C. (C.) *cinereus* Theo.

Whilst this species was commonly found breeding in tree holes, unlike *C. nebulosus* it never occurred in utensils. Large numbers of larvae were found in disused dye pits at Zaria City.

C. (C.) *cinerellus* Edw.

A male and female were reared from material in a calabash left in a small forest.

C. (C.) *macfiei* Edw.

Larvae have only been found by the writer in two tree holes.

C. (*Mochthogenes*) *inconspicuus* (Theo.).

A single female was found resting under a fallen tree in a forest.

C. (Culex) poicillipes (Theo.).

Small numbers of adults were regularly taken during the dry season while biting man at night. Larvae were common in ground pools and borrow pits.

C. (C.) ethiopicus Edw.

A single female was reared from a pupa found in an open swamp.

C. (C.) annulioris Theo.

Larvae were common in pools, frequently associated with filamentous algae.

C. (C.) duttoni Theo.

Larvae were often found in domestic utensils and pools, generally in foul water.

C. (C.) univittatus Theo.

Larvae were frequent in small pools and holes in river banks.

C. (C.) pipiens fatigans Wied.

Breeding was very common in pit latrines in Kaduna and the adults usually rested inside huts; on one occasion 760 adults were collected from a single room. This species is by no means completely anthropophilous in the area. Fed females taken from horse and goat stables were found by precipitin tests to have fed on those animals. A large number of fed females was collected resting in crab-holes in Kaduna; the bloods were found to be negative for man and domestic animals, and the writer is of the opinion that these individuals were feeding on the toad, *Bufo africanus*, which was common in the crab-holes.

C. (C.) antennatus (Becker).

Larvae were frequent in weedy pools.

C. (C.) decens Theo.

Larvae were very common in pools and borrow pits and sometimes found in utensils and tree holes.

C. (C.) trifoliatus Edw.

During August 1958, several adults were taken resting amongst low vegetation in a fringing forest.

C. (C.) perfuscus Edw.

Recorded by Mattingly (1947).

C. (C.) guiarthi Blanch.

Recorded by Mattingly (1947).

C. (C.) perfidiosus Edw.

Recorded by Mattingly (1947).

C. (C.) weschei Edw.

Larvae were found by the writer on two occasions, in a rock pool with emergent vegetation and in a flood pool.

C. (C.) grahami Theo.

Larvae were fairly frequent in rock pools and small temporary ponds.

Toxorhynchites brevipalpis var. **conradti** Grünb.

A very common tree-hole breeder, larvae were also found by the writer in clay pots placed in wooded areas and on one occasion in a tin can. Larvae generally occurred singly although up to six have been found in a single pot. That the larvae are important predators of other mosquitos was demonstrated when, in the laboratory, three fourth-stage larvae devoured 118 fourth-stage larvae of *Aedes aegypti* in six days.

T. viridibasis Edw.

A single specimen was bred from material collected in a tree hole in 1957 (W. A. MacDonald, personal communication).

2

**PENTALITOMASTIX, A NEW NAME FOR PSEUDOLITOMASTIX EADY
(HYMENOPTERA, CHALCIDOIDEA).**

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The name *Pseudolitomastix* was applied (Eady, 1960) to a genus erected for the new species *P. nacoieiae*, bred from *Nacoieia octasema* (Meyr.). This unfortunately overlooked the valid and prior use of the name *Pseudolitomastix*, by Risbec (1954). The two species for which *Pseudolitomastix* Risbec was erected are generically quite distinct from *P. nacoieiae*, so that a new generic name is required for this latter species. The name *Pentalitomastix*, indicative of the five-segmented funicle of the female antenna, is hereby proposed. I am grateful to Dr. O. Peck, of the Entomology Research Institute of the Canadian Department of Agriculture, for drawing my attention to the homonymy, and to my colleague Mr. G. J. Kerrich for suggesting the new name.

Family ENCYRTIDAE.

Genus **Pentalitomastix**, n.n.

Pseudolitomastix Eady, 1960, Bull. ent. Res. **50** pp. 667-670.

Pentalitomastix nacoieiae (Eady).

Pseudolitomastix nacoieiae Eady, 1960, Bull. ent. Res. **50** pp. 667-670.

References.

- EADY, R. D. (1960). A new genus and two new species of Encyrtidae (Hymenoptera, Chalcidoidea) from the banana scab moth, *Nacoieia octasema* (Meyr.).—*Bull. ent. Res.* **50** pp. 667-670.
- RISBEC, J. (1954). Chalcidoïdes et Proctotrupides de l'Afrique tropicale française (4^e supplément).—*Bull. Inst. franç. Afr. noire* (A) **16** pp. 1035-1092.

MOVEMENTS OF THE VECTORS OF VIRUS DISEASES OF CACAO IN GHANA.

II.—WIND MOVEMENTS AND AERIAL DISPERSAL.

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(PLATES VII & VIII.)

CONTENTS.

	PAGE
Wind movements in Ghana	176
More detailed studies at Tafo	177
Day-to-day variations in wind speed	177
Diurnal changes in wind speed	178
Daily wind speeds in cacao	179
Air movement at different elevations in cacao	179
Laboratory studies of vector dispersal	180
The aerial movement of mealybug vectors in the field	181
Trapping methods	183
A demonstration of mealybug aerial movement in cacao	183
The elevation of movement in cacao	183
Distance of movement in cacao farms	186
Dispersal over greater distances from cacao	188
Seasonal changes in aerial dispersal	191
The establishment of airborne mealybugs on cacao	193
On cacao seedlings	194
On cacao trees	194
Discussion	197
Summary	199
References	200

In an earlier paper (Cornwell, 1958) two types of spread of the viruses causing swollen-shoot disease of cacao were described: (1) radial spread from the edges of established outbreaks, and (2) 'jump spread' with the formation of new infections at varying distances from existing outbreaks, sometimes in otherwise unaffected areas. Studies of the mobility of the dominant mealybug vector, *Pseudococcus njalensis* Laing, on individual trees and between trees (Cornwell, *op. cit.*) suggested that the first type of spread could be explained by vectors moving through the interlocking canopy formed by mature cacao at normal spacings. The present paper details experiments carried out to investigate to what extent involuntary aerial dispersal of vectors, under the influence of wind, may account for the patterns of virus infection described.

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Wind movements in Ghana.

The only published information on the distribution and seasonal changes of wind movement in Ghana was recorded by the Ghana Meteorological Department (Walker, 1957) at seven representative stations between 1944 and 1953. Three

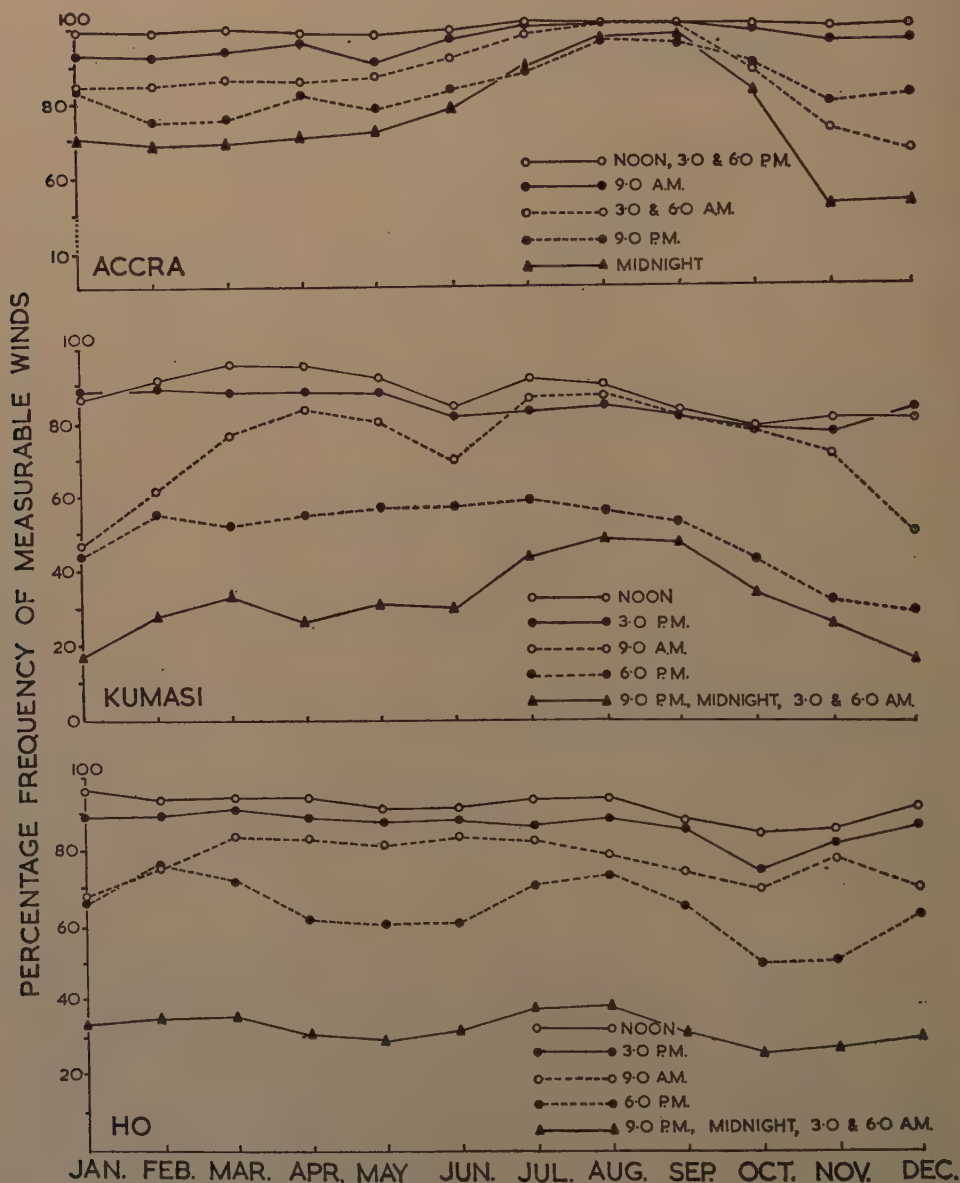


Fig. 1.—Frequency of measurable winds (force 1 and above) at different times of the day, summarised by months. Percentages are based on totals of 250–300 observations at each synoptic hour between 1944 and 1953. Measurements at Accra and Kumasi were made with Dines' pressure-tube anemometers and observations at Ho were made visually. (From Walker, 1957.)

of these, Accra, Kumasi and Ho, lie near or within the cacao-growing areas. Wind movements at Accra (20 miles outside the southern limit of cocoa production) are influenced by its coastal position, but data from the other stations (central Ashanti and southern Togoland, respectively) may be considered characteristic of the forest belt.

The frequencies of measurable winds (force 1 and above) at different times of the day are presented, by months, for the three stations (fig. 1). At all locations, measurable speeds are most frequent between 9 a.m. and 3 p.m. G.M.T. and minimal between 9 p.m. and 6 a.m., these differences being more marked inland than on the coast. Changes in the frequency of measurable speeds during the year are small; they are most marked at Accra, with maxima during August and September and minima during November and December. These periods are associated with high and low frequencies of winds above force 3 (60–80% and 20–40% at midday, respectively). Data recorded at Kumasi and Ho show that measurable winds occur slightly more frequently from March to May and during February and March, respectively, and again during July and August at both stations. Inland, these periods are associated with slightly higher frequencies of speeds above force 3 (about 5% at Kumasi and 10–20% at Ho). At these stations, the frequency of measurable winds is lowest from November to January and between October and November, respectively.

The prevailing wind over most of Ghana is south-westerly, veering between south and west at different times of the day. Changes in direction are also most marked on the coast. The north-easterly Harmattan, characteristic of the dry season (December–February), varies in severity from year to year and is frequently never felt in the southern half of the country.

Winds at Tafo, in the Eastern Province, may be divided into two distinct categories: gentle breezes, which are experienced throughout the year, and extremely strong winds of short duration which precede falls of heavy rain, particularly during March and April. These strong winds have not been studied in detail; they are maintained for periods of 5 or 10 minutes and gusts are estimated to reach gale force of 60 m.p.h. Wind direction at Tafo is influenced by its proximity to the southern scarp (3,000 ft.), winds from the north-east occurring more frequently than those from the south.

More detailed studies at Tafo.

Two instruments were available for measuring air currents at Tafo: a cup anemometer sensitive to wind speeds greater than 0.83 m.p.h. and a vane anemometer capable of recording the slightest air displacement. The latter instrument was attached to a 3-ft. triangular directing vane, counterbalanced by heavy weights, the whole turning into the wind when suspended on a fine wire (Pl. VII, fig. 1). A correction factor for the cup anemometer was obtained by recording wind speeds with the two instruments simultaneously, under controlled conditions in the laboratory and during 24-hour periods in the field.

Day-to-day variations in wind speed.

The cup anemometer was first used in a clearing to examine variation in the daily wind run at four ft. above the ground. Records were taken at 9 a.m. on six consecutive days each week from the middle of April to the end of November 1955. The distribution (fig. 2 a) shows a wide range of speeds, which varied from 14.9 to 43.8 miles per day, with an over-all mean of 27 (= 1.1 m.p.h.). Analysis of the variation within and between weeks showed significant changes in wind speed between the five-day periods ($P < 1\%$): the mean daily speeds for periods 2nd–7th May, 18th–23rd July and 8th–13th August exceeded the over-all mean by twice its standard error (± 2.09), while those for periods 14th–19th and 21st–

26th November were correspondingly less. Thus, variations in the wind run at Tafo occurred at about the same time of the year as changes in the frequency of winds demonstrated by the nine-year data for Kumasi.

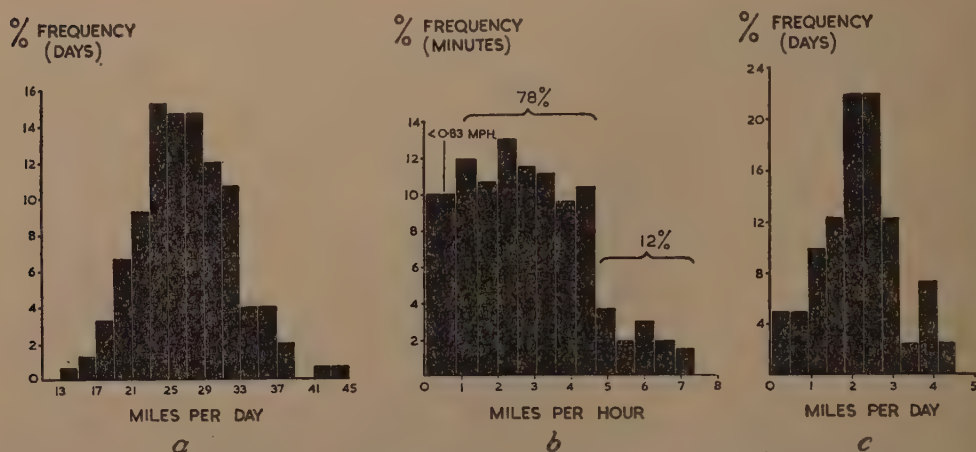


Fig. 2.—Frequency distributions of wind speeds: (a) on 150 days in a clearing at four ft. above the ground; (b) in 270 one-minute periods between 8.30 a.m. and 5.30 p.m. under the same conditions as (a), the width of each histogram column but the first representing 0.55 m.p.h.; (c) on 41 days in cacao at eight ft. above the ground.

Diurnal changes in wind speed.

At the same location, wind speeds were recorded at half-hourly intervals between 9.0 a.m. and 4.0 p.m. on six days during the last week of February 1955. There was a gradual increase in the average speed from 2.3 m.p.h. to a maximum, between 2.30 and 3.0 p.m., of 4.7 m.p.h., which was higher ($P < 1\%$) than means recorded before 12.30 p.m. and after 3.30 p.m. (fig. 3). Records

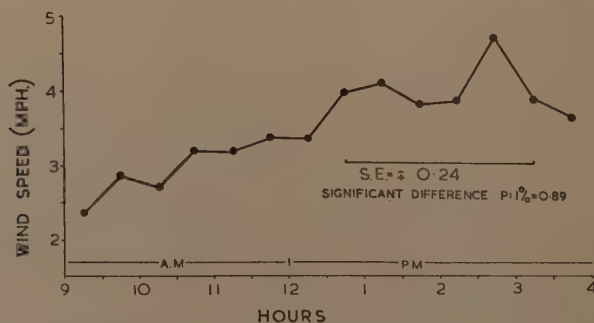


Fig. 3.—Six-day means of wind speed recorded daily for corresponding half-hourly periods between 9.0 a.m. and 4.0 p.m. during the last week of February 1955.

were also taken of wind runs on 17 days during June, for the six-hour period 9.0 a.m. to 3.0 p.m. and the 18-hour period 3.0 p.m. to 9.0 a.m. Means of 2.02 ± 0.09 m.p.h. and 0.87 ± 0.04 m.p.h., respectively, were recorded.

Wind speeds during alternate one-minute periods were also examined, using the same instrument, on two days at the end of the dry season. Accurate

measurements were obtained by counting the cup rotations. On the first occasion (26th Feb. 1955), wind speeds were recorded for 100 periods between 8.30 a.m. and 11.50 a.m., after which observations were discontinued because of torrential rain. During 9 per cent. of the periods there was no movement of the anemometer (winds of less than 0.83 m.p.h.). Winds of 0.8 to 4.7 m.p.h. were recorded during 80 per cent. of the periods and speeds greater than this during 11 per cent. On the second occasion (28th Feb.), speeds were recorded during 270 alternate one-minute periods between 8.30 a.m. and 5.30 p.m., and the results (shown as a frequency distribution in fig. 2 b) provided the comparable percentages of 10, 78 and 12 for the three wind-speed categories.

Daily wind speeds in cacao.

Measurements of wind in farmers' cacao were made using the vane anemometer suspended 8 ft. above the ground in a break in the canopy. Wind runs over 24 hours were recorded on 41 days in April and May 1955, and their frequency distribution is shown in fig. 2 c. The recorded wind speeds ranged from 0.35 to 4.1 miles per day with a mean of 2.2 miles. Clearly, wind movement in the canopy is much less than away from cacao (fig. 2 a), and the magnitude of this difference was estimated by recording speeds under the two conditions simultaneously. This was done on 26 days during April and May at sites less than half a mile apart. From a significant correlation between the data for the two instruments ($r = +0.74$, $P < 0.1\%$) the following relationship was obtained.

Daily wind runs (miles per day)	
In cacao canopy (8 ft.) (vane anemometer)	In clearing (4 ft.) (cup anemometer)
0.1	20.5
1	23.7
2	27.2
3	30.8
4	34.3
5	37.8

While this method provides only an approximate comparison, it indicates that, with average wind speeds prevailing, the velocity in cacao (2.2 miles per day, or 0.09 m.p.h.) is about one-tenth of that outside, while on calmer days (1 mile per day) it may fall to one-twentieth.

Air movement at different elevations in cacao.

In a later section, an experiment is described in which the aerial dispersal of Coccids was examined at various elevations in cacao. During this study, records were made of wind movement at eight levels, from 2 to 30 ft. above ground, at two sites less than 50 yd. apart, and comparable with the types of trapping location: one with a closed canopy from 15 to 25 ft. up, in which a circular hole of four ft. diameter was cut to allow movement of the vane anemometer, and the other at the centre of a break in the canopy, some 20–30 ft. across, where a few virus-infected trees had been cut out. Two 24-hourly wind runs were recorded at each level and at each site during October and November 1955. Using only one instrument it was necessary to allocate the levels to days and to measure the run of wind at each position in random sequence.

The results show striking differences in the pattern of air movement at the two sites (fig. 4). For the closed canopy, maximum air movement was recorded at two feet above the ground and the lowest speeds in the levels of the canopy, just above which the mean air speed was comparable to that at 10 ft. and slightly lower than at 2 ft. Where the canopy was open, air movement was greatest above

it and lowest at two feet above the ground; there was a marked drop within the canopy, though the mean speeds at these levels were considerably higher than for the closed canopy.

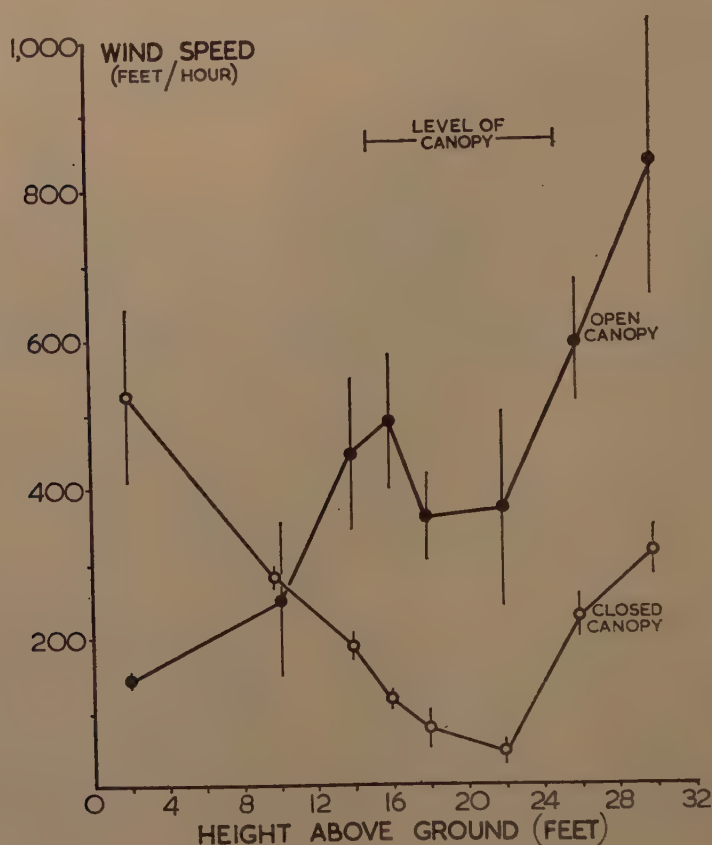


Fig. 4.—Distributions of wind speed at different elevations in cacao with open and closed canopies, showing the mean and range of two 24-hourly measurements at each level.

Laboratory studies of vector dispersal.

Colonies of *Ps. njalensis*, covered by carton tents made by ants, on cut cacao were exposed to air currents of 10 m.p.h. Mobile mealybugs of all instars, walking on green, unhardened twigs and on second-year tissues, were treated similarly. In some tests the air speed was increased gradually and in others the insects were exposed suddenly to the maximum. In either event, the colonies and their coverings remained intact, while the mobile insects held fast to the twig, flattening themselves against the surface. However, mealybugs walking on cacao are easily removed by gently tapping the twig, and the following experiment was designed to compare the ease of removal of different instars of four species.

Mealybugs were placed singly on a piece of cacao twig which was pivoted loosely at its centre and balanced horizontally. The insects were allowed to walk on a particular area of the twig, which was then given a glancing tap at one end

by a hinged hammer falling from rest. If the insect was not removed the force of the tap was increased by adding weights to the hammer. Results obtained for the instars of *Ps. njalensis*, *Planococcus citri* (Risso), *Ferrisia virgata* (Ckll.) and *Pseudococcus gahani* Green, are shown in Table I and fig. 5. Analysis of

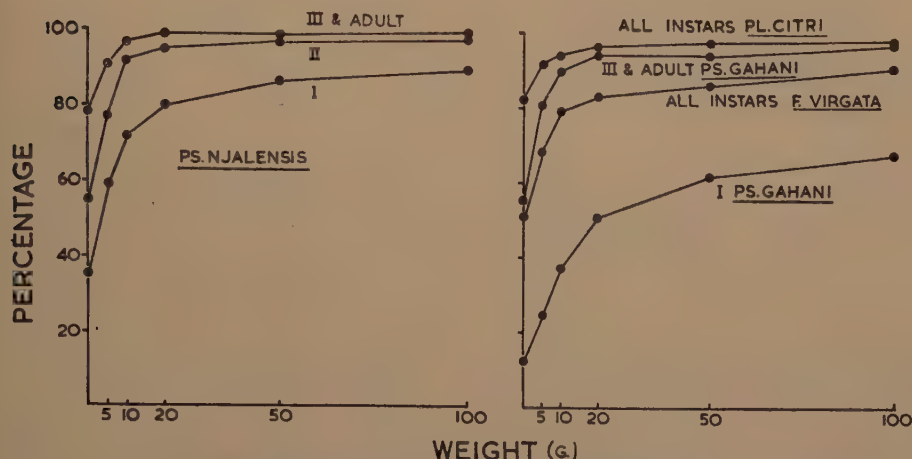


Fig. 5.—Accumulated percentages of test insects dislodged from cacao by tapping a twig with increasing force (see text and Table I).

the data by the chi-squared test * showed significant differences between successive instars of *Ps. njalensis*, the older ones being most easily dislodged. First-instar nymphs of *Ps. gahani* were also more difficult to remove than the third and adult stages, but these differences were not found in *Pl. citri* or *F. virgata*. Differences between the first-instar nymphs of *Ps. njalensis* and *F. virgata* ($\chi^2 = 7.7$) were not significant, but those of the former were more readily dislodged than 'crawlers' of *Ps. gahani* ($\chi^2 = 35.3$, $P < 0.1\%$). At this same level of probability, first-instar nymphs of *Pl. citri* were more readily removed than those of the three other species.

These observations indicate that average winds in cacao are unlikely to be directly responsible for removing mealybugs from their plant hosts, particularly when protected by ant-made tents. More probably, mobile individuals become dislodged by movement of the twigs and are then carried away by air currents when falling from the canopy. Because first-instar nymphs of *Ps. njalensis* make up 92 per cent. of the mobile population (Cornwell, 1958) and they are of very light weight (mean 3.2×10^{-6} g.), this stage may be well represented in the aerial population: older instars are more readily dislodged but, being heavier (second instar 29, third 43, young adults 117×10^{-6} g.), they may be windborne over shorter distances. The results also indicate that nymphs of *Pl. citri* may be more readily dispersed than those of other species.

The aerial movement of mealybug vectors in the field.

An examination was made of the aerial movement of mealybugs within and at various distances from farmers' cacao. Some experiments were continued over many months to provide information on seasonal changes in dispersal.

* Applied after grouping the data to provide expected class frequencies of not less than five.

TABLE I.
Numbers of mobile mealybugs dislodged from a cacao twig by gentle tapping.

Species	Instar	Number tested	Number dislodged from twig								No. not removed	Chi-squared	Probab- ility (%)
			by hammer only	by additional weights (g.) +5 +10 +20 +50 +100									
<i>Ps. njalensis</i>	I	158	56	38	19	13	11	5		16	} 22.7 } 17.2	<0.1 <0.1	
	II	128	70	20	3	3	2		2				
	III + Adult	141	110	18	9	2	1	1	0				
<i>Pl. citri</i>	I	80	68	6	1	1	1	1		2	} 1.55	Non-sig.	
	II	43	36	4	1	1	1	0	0				
	III + Adult	66	51	8	2	3	0	0	2				
<i>F. virgata</i>	I	89	39	15	12	2	5	6		10	} 6.3	Non-sig.	
	II	56	27	13	6	4	0	1	5				
	III + Adult	60	36	8	4	3	2	2	5				
<i>Ps. gahani</i>	I	91	11	11	12	12	10	6		29	} 34.8	<0.1	
	III + Adult	31	17	8	3	1	0	1	1				

Trapping methods.

Three types of trap were used:

Pieces of fresh cacao twig (previously fumigated in a hydrogen cyanide chamber) were attached to trees for 24-hourly periods, as described by Cornwell (1958). The twigs were examined in the field for mealybugs, under a binocular microscope.

Sticky traps, prepared from tins 4" high and 3" base diameter, banded with paper and coated with 'Ostico' grease, were exposed for fortnightly periods and returned to the laboratory for examination under a hand lens. Coccids were removed, freed from grease in a mixture of ethyl acetate and glacial acetic acid, and mounted for identification. The tins were rebanded and greased before being used again.

Cacao seedlings in baskets were exposed at fixed positions and examined for mealybugs at intervals. Other seedlings of standard heights in boxes were exposed for fortnightly periods, examined in the field and fumigated before further exposure. Alternatively, cacao beans were sown in small plots at 4-weekly intervals and the seedlings examined for mealybugs when 8 weeks old.

A demonstration of aerial movement of mealybugs.

Preliminary observations were made by attaching bait twigs to dead cacao trees during April and May 1955. Four cacao trees, free from mealybugs, were felled at ground-level and the leaves allowed to wilt. These trees were then 'planted' as close as possible to living ones supporting high mealybug populations, short of the branches actually touching, and their trunks were grease-banded at ground-level. Twenty-four pieces of fresh cacao twig were attached in pairs to each experimental tree, at one ft. above the ground and at two-ft. intervals up the trunk and along the branches as described previously (Cornwell, *op. cit.*). Trapping was carried out on 40 days, during which 38 mealybugs were recorded, 28 being first-instar nymphs and about equal catches being obtained at the different levels. Identified specimens were *Ps. njalensis*, *Ps. comstocki* (Kuw.) and *Pl. celtis* (Strickl.).

The elevation of movement in cacao.

Aerial dispersal of Coccids at different heights in farmers' cacao was examined by using sticky traps at seven levels from 2 to 30 ft. above the ground. Four pairs of sites were selected to compare aerial movement in a closed canopy (Pl. VII, fig. 2)—a continuous layer of interlocking branches extending from 15 to 25 ft. above the ground—and in an open canopy where diseased trees had been removed during routine 'cutting-out' operations. In the closed canopy, a hole four ft. wide was cut through the branches to allow the erection of traps; the break in the open canopy was 20 to 30 ft. across.

Traps at the various levels were suspended on a cable, which was supported on pulleys mounted at the top of a vertical pole (Pl. VII, fig. 3). The bottom of the cable was pegged to the ground and both attachments were grease-banded. There were four traps at each level, held horizontally on wooden cross-bars, with the trapping surfaces 8 to 12 in. from the central cable. The trapping surface was divided into four equal sections, 'top', two 'sides' and 'bottom' (Pl. VII, fig. 4), to provide information on the direction of movement of the vectors at different levels.

The traps were first exposed during October 1954 and renewed at fortnightly intervals until April 1956. Only one site was worked per day, the sites being visited in sequence and weeds growing round the base of the structure cleared at each visit. When changing the traps, they were lowered to the ground, the bottom ones removed first as they came within reach and the top ones replaced first as the cable was raised. All traps were carried between the laboratory and

the field in closed boxes to preclude contamination in transit. The distributions of 171 mealybugs and 125 other Coccids caught during the experiment are shown in Tables II and III.

TABLE II.

Numbers of mealybugs and other Coccids caught on sticky traps at different elevations in cacao.

Elevation (ft. above ground)	Mealybugs				Other Coccids			
	Type of canopy							
	Closed		Open		Closed		Open	
	Σn	$\Sigma \log(n+1)$	Σn	$\Sigma \log(n+1)$	Σn	$\Sigma \log(n+1)$	Σn	$\Sigma \log(n+1)$
2	48	10.33	2	0.60	34	7.92	11	2.58
10	44	10.32	1	0.30	10	2.88	6	1.80
14	17	4.18	3	0.78	10	2.88	3	0.90
16	17	4.60	6	1.80	10	2.46	3	0.90
18	13	3.48	5	1.38	9	2.70	6	1.68
22	4	1.20	1	0.30	7	1.98	8	1.90
30	8	2.28	2	0.60	6	1.68	2	0.60
Total	151	36.39	20	5.76	86	22.50	39	10.36
Sites	Totals for paired sites							
A	5	1.50	6	1.68	37	10.08	10	2.88
B	71	17.94	8	2.40	5	1.50	6	1.30
C	14	4.08	5	1.38	30	6.96	20	5.28
D	61	12.87	1	0.30	14	3.96	3	0.90

Σn = arithmetic total, $\Sigma \log(n+1)$ = logarithmic total, where n_1, n_2, \dots = no. of Coccids caught in trapping periods, 1, 2, . . . etc.

The first point of interest is the size of the catches, which were much smaller than those obtained by Strickland (1950), using comparable methods. He removed all insects for identification, whilst, in the present study, traps were examined for Coccids only, and undoubtedly many escaped detection. The second point of interest concerns the relative abundance of different instars; for mealybugs the proportions, in percentages, were, first instar 6, second 80, third 6 and adults 8. These proportions are not comparable with those obtained for live catches on bait twigs. It is probable that, on sticky traps, first-instar nymphs could not be so readily detected because of their small size and the accumulation of vegetable debris on the trapping surface.

For statistical analysis, the catches for each trapping period were transformed to $\log(n+1)$ and summed for trapping levels. These figures were further summed to give transformed totals for trapping site and condition of the canopy. Analysis of the transformed data (Table II) showed significant differences in catch between pairs of sites for both mealybugs ($P < 1\%$) and other Coccids ($P < 5\%$). Furthermore, larger catches of both groups were recorded in the presence of a closed canopy than an open one (mealybugs $P < 0.1\%$, other Coccids $P < 5\%$); this may have been caused by the difference in proximity of traps to infested trees. Support for this suggestion is given by the negative correlation ($r = -0.98$; $P < 2\%$) between the catches of mealybugs and other Coccids at the four closed-canopy sites. These groups are known to be negatively associated on cacao (Strickland, 1951).

Further analysis showed a significant interaction ($P < 5\%$) between the numbers of mealybugs caught at different levels and the condition of the canopy. Whilst catches from the open canopy were too small to show significant differences with elevation, it is of interest to note that the highest catches were obtained at 16 and 18 ft., level with the canopy. For the closed canopy, catches were greater at

TABLE III.

Distributions of mealybugs and other Coccids on the surface of sticky traps at different elevations in cacao.

(Combined data for traps in open and closed canopies.)

Elevation (ft. above ground)	Mealybugs			Other Coccids*		
	Position on trap					
	Top	Sides	Bottom	Top	Sides	Bottom
2	12	35	3	25	11	9
10	19	26	0	8	6	2
14	10	9	1	5	6	2
16	10	9	4	5	6	1
18	6	12	0	2	8	3
22	1	3	1	8	7	0
30	2	7	1	2	4	2
Total	60	101	10	55	48	19

* The positions of three specimens were not recorded.

2 and 10 ft. than at 14, 16 and 18 ft. ($P < 5\%$) and still greater than those at 22 and 30 ft. ($P < 1\%$). Differences in the catches of other Coccids at the various levels were not significant, but their numbers also decreased with height, particularly for the closed canopy.

The chi-squared test was used to analyse the distribution of catches over the surface of the traps (fig. 6). To do this, it was necessary to group the data for the higher trapping levels, because catches were so few. It was considered unnecessary, however, to make a correction for each trap having one top and one bottom, but two sides. The analysis for mealybugs showed that the numbers caught on the three portions varied with trapping level ($\chi^2 = 13.2$, $P < 5\%$), more being caught on the upper part of the trap in or below the canopy than at other levels. Conversely, at the 2-ft. and 18-30-ft. levels a higher proportion of catches was on the sides of the trap. The analysis for other Coccids provided no evidence of heterogeneity, although at the different levels there were slight changes in distribution which differ from those shown for mealybugs.

The results of this experiment must be considered together with the data obtained for wind movement in cacao (fig. 4), which show that, for a closed canopy, wind speed above cacao (30 ft.) is similar to that at the 10-ft. level, while above an open canopy it is higher than at all lower levels. Yet, of total catches, only 6 per cent. of both mealybugs and other Coccids were recorded above the canopy, compared with 26 per cent. of mealybugs and 13 per cent. of other Coccids caught at the 10-ft. level. This marked difference for mealybugs would suggest that these insects are not commonly carried upwards by air turbulence and that those from the forest trees, under which cacao in Ghana is normally grown, do not contribute substantially to the aerial population in farms. Also, more air movement was recorded where diseased trees had been felled than where the canopy remained intact. Yet, of the total catches, only about 12 per cent. of

windborne mealybugs and 31 per cent. of other Coccids were caught at the former sites. This would indicate that, for mealybugs at least, airborne insects are not dispersed many feet from infested trees. Moreover, at 10 and 15 ft. below the canopy, a higher proportion of mealybugs (42 and 46%) were caught on the 'tops' of the traps than would be expected from the proportion of total trapping area (25%) which these constitute. At the 2-ft. level, however, the proportion of

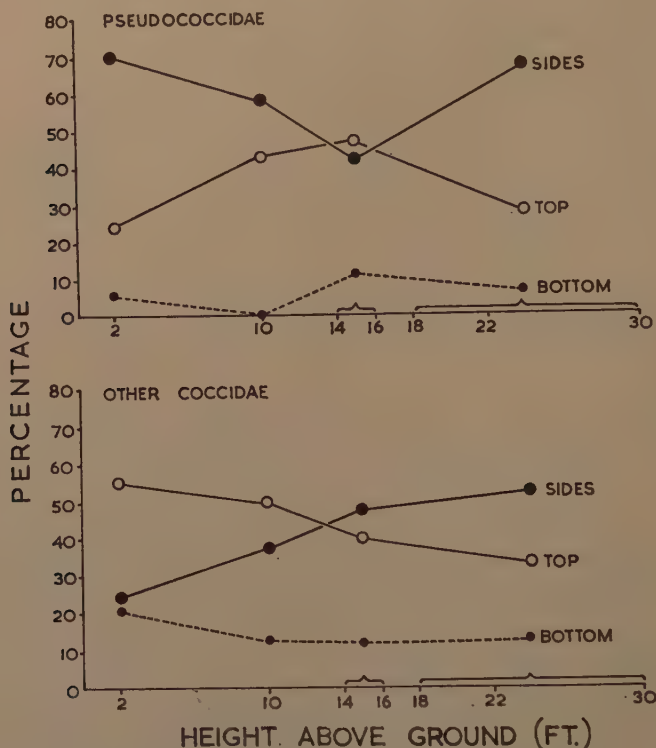


Fig. 6.—Distributions of mealybugs and other Coccids over the surface (top, bottom, sides) of sticky traps at different elevations in cacao. Combined data for open- and closed-canopy sites.

catches on the top portion (24%) approximates very closely to the expected value. This confirms the suggestion that mealybugs drop from the branches and are carried by air currents when falling. Larger catches 2 ft. above ground, with a high proportion of these (70%) on the sides of the traps, indicate that the density of mealybugs being laterally dispersed is greatest at this level, where (as shown earlier) wind speed under a continuous canopy is greatest. The disparity between some of the results obtained for mealybugs and other Coccids is not fully understood, but may reflect the marked differences in ecological niche which these two groups occupy.

Distance of movement in cacao farms.

The distance of mealybug dispersal in cacao was studied by using as traps groups of three basket seedlings placed on the ground, allowing ants to aid the establishment of windborne mealybugs: experience had shown that ants only

infrequently transport mealybugs (Cornwell, 1956, 1958). Two sites were selected for comparison: one, a block of mealybug-infested cacao with a closed canopy, the other, an area of clean-weeded soil where cacao had been removed two years earlier. At the latter site the forest trees remained standing and the area was

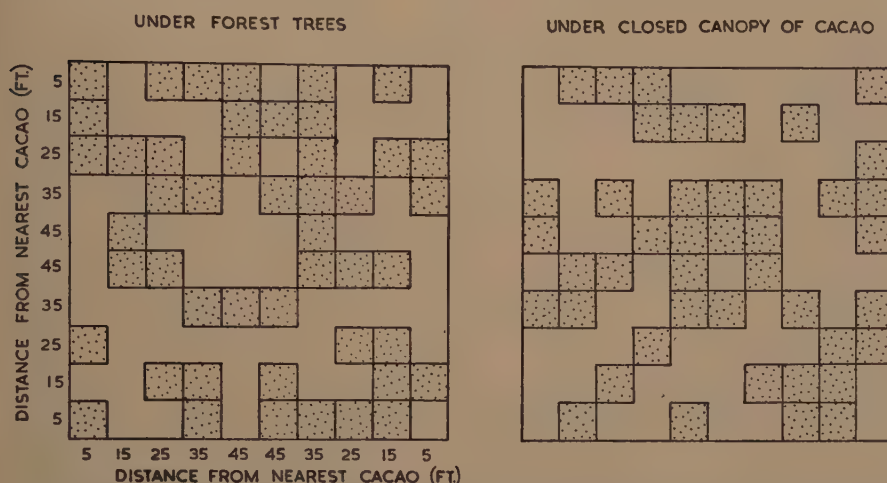


Fig. 7.—Distribution of infested traps (three basket seedlings per site) placed on bare soil, (a) under the canopy of forest trees and surrounded by mealybug-infested cacao, (b) under a continuous canopy of infested cacao.

completely surrounded by coppiced cacao bearing infested chupons (water shoots). Both plots were square with 100-ft. sides, and the traps were set out in lines at 10 × 10 ft. spacing. In the cleared site the outer traps were 5 ft. from the nearest cacao. No precaution was taken against the possible movement of mealybugs across the ground, since it had been shown that the soil surface restricts

TABLE IV.

Observed numbers of seedling traps infested by mealybugs, (a) under forest trees and surrounded by infested cacao and (b) under the closed canopy of infested cacao. (These distributions are compared with expected distributions based on random dispersal.)

No. of traps	Under forest trees and surrounded by infested cacao		Under the closed canopy of infested cacao		
	Distance from nearest cacao (ft.)	Numbers of traps infested		Observed	Expected
		Observed	Expected		
36	5	18	16.9	15	15.1
28	15	13	13.2	12	11.8
20	25	8	9.4	4	8.4
16	35+45	8	7.5	11	6.7
100		47		42	
χ^2		0.32, $P=95-98\%$ (N.S.)		5.07, $P=10-50\%$ (N.S.)	

terrestrial movement (Cornwell, 1956). Traps were exposed on the 14th March 1955 and examined eight weeks later.

The patterns of infestation obtained at the two sites are shown in fig. 7; the numbers of traps infested at different distances from the edges of the plots are shown in Table IV, together with the expected number based on random distribution. Comparison of the observed and expected distributions by the chi-squared test indicates no significant relationship between infestation rate and position of the traps—in fact the data for the cleared area show an extremely close agreement with the expected distribution. Under the canopy of standing cacao there was a slightly greater difference between the two distributions, probably caused by the discontinuous pattern of infested trees, a feature characteristic of mealybug populations, noted by Strickland (1951).

It is evident from the results of this experiment that distances of less than 45 ft. do not prevent the infestation of cacao seedlings by airborne mealybugs. The proportions, in percentages, of traps infested by different species in the cleared area were: *F. virgata* 26, *Pl. citri* 35 and *Ps. njalensis* 39. The corresponding figures for traps under cacao were: *F. virgata* 9, *Pl. citri* 68 and *Ps. njalensis* 23. The proportions, at the two sites, are not significantly different at the 5 per cent. level of probability.

Dispersal over greater distances from cacao.

In a preliminary experiment to examine the wider dispersal of mealybugs, 15 groups of basket seedlings were exposed at various distances between 27 and 360 ft. from the nearest cacao on the West African Cocoa Research Institute's water reservoir. This location was chosen to ensure complete insulation from ants. Before exposure, the seedlings were sprayed twice with ammoniated nicotine sulphate solution to eliminate mealybug contamination. They were exposed in early November 1952, and examined at intervals until the middle of February 1953. Forty-five mealybugs were recorded at 11 sites; 35 were reared successfully to the adult stage and identified as follows:

<i>Ps. njalensis</i>	1
<i>Pl. citri</i>	18
<i>F. virgata</i>	11
<i>Pseudococcus hargreavesi</i> Laing *	2
<i>Ps. comstocki</i>	2
<i>Planococcus kenya</i> (Le Pelley)	1

Slightly more than one-third of the insects was taken on the two traps nearest to cacao (distances of 27 and 42 ft.), whilst at the maximum distance at which catches were obtained (340 ft.), two mealybugs only were recorded. At one site an ovisac was found in the absence of an adult.

In a second experiment on the reservoir certain improvements were made. It had been found that seedlings exposed to high insolation, caused by reflection from the water, soon became unsuitable for trapping mealybugs. As it was feared that shade placed over the traps might influence the catches, it was decided to expose seedlings for fortnightly periods only and to 'rest' them in the shade of an insectary for a further two weeks before re-use. The preliminary experiment had also shown that any mealybugs overlooked when the seedlings were examined reproduced to give a misleading estimate of the number of airborne mealybugs at the next examination. This was overcome by fumigating the seedlings with hydrogen cyanide for half an hour every time they were about to be exposed. They were then carried the mile between the laboratory and the reservoir in covered transport to prevent contamination in transit.

* This is the species referred to by earlier authors (cf. Strickland, 1947) as *Ps. bukobensis* Laing, which Williams (1958) has shown to be a synonym of *Ps. hargreavesi*.—Ed.

For this experiment, 30 oil drums were sunk into the water, leaving a few inches exposed above the surface. They were placed not less than 50 ft. apart along one-third of a mile off the north bank at different distances from cacao (Pl. VIII, fig. 1). Ideally, it would have been preferable to arrange the sites at varying distances from one point on the bank, but the terrain did not allow this. Each drum was covered by a wooden platform to support five boxes, each containing 10 seedlings. These were first exposed when six months old, examined two weeks later, and replaced by further seedlings from the insectary. Only three sites were worked each day, these being selected at random in the first instance and thereafter examined systematically. All boxes were numbered so that they could be returned to the appropriate site. Transplants were made to replace dead seedlings.

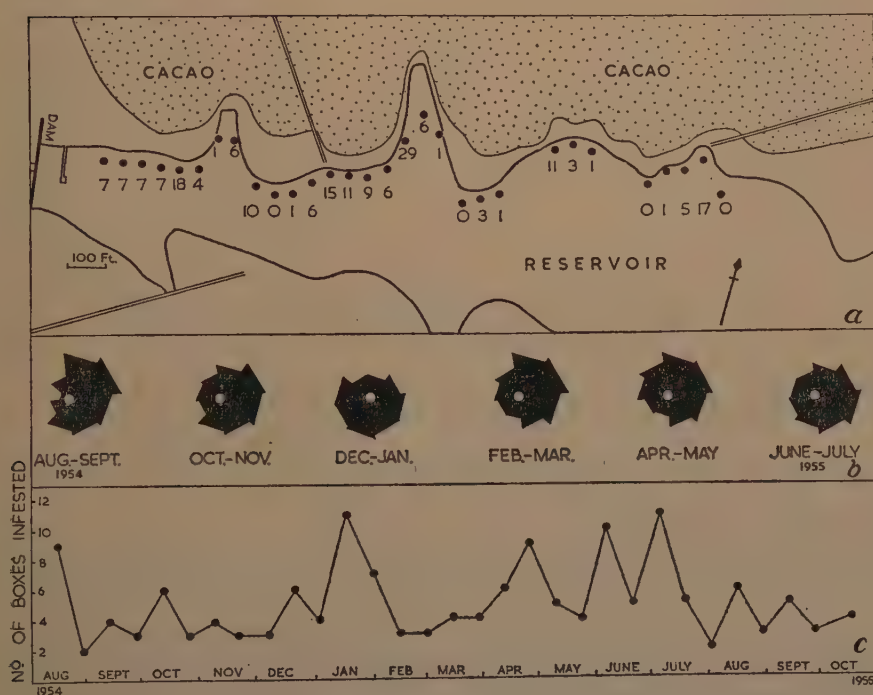


Fig. 8.—(a) The arrangement of trapping sites on the W.A.C.R.I. reservoir at different distances from cacao, with catches of mealybugs at each site indicated; (b) the frequency of wind directions during two-monthly periods; (c) seasonal changes in dispersal represented by changes in the number of boxes of cacao seedlings infested during fortnightly trapping periods.

Thirty-one fortnightly examinations were made between August 1954 and October 1955, during which period 193 mealybugs were caught. Observations on seasonal changes in catch (fig. 8 c) are examined in a later section. The distribution of catches along the bank is shown in fig. 8 a, together with the frequency of wind directions for two-monthly periods (b). The catches for each fortnightly period were transformed to $\log(n+1)$ and summed for trap position. The trans-

formed totals are plotted against distance of the traps from the nearest cacao in fig. 9.

There was an over-all decrease in catch with distance, but the correlation ($r = -0.34$) is of low significance ($P < 10\%$). This is not surprising because of probable differences in mealybug population on the cacao along the bank; where numbers are low, even the nearest traps would provide small catches. Moreover,

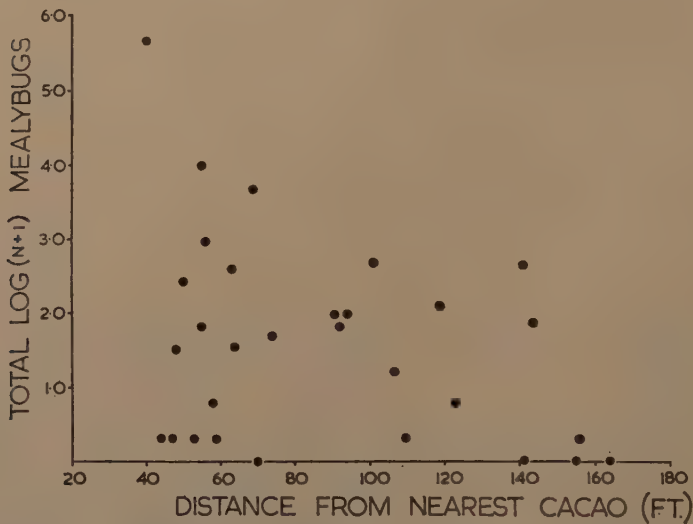


Fig. 9.—Catches of mealybugs on seedling traps on the W.A.C.R.I. reservoir at different distances from cacao. Total catch = $\sum \log (n + 1)$ mealybugs, where n_1, n_2, \dots, n_{31} = catches during 31 fortnightly trapping periods.

mealybugs reaching the traps may have been blown from greater distances within the cacao, masking the effect of distance from the bank. Catches included *Ps. njalensis*, *Dysmicoccus brevipes* (Ckll.) and *F. virgata*, but the majority belonged to the *Planococcus citri/kenyae* group. All instars were represented in about equal numbers. This suggests that younger stages were more abundant on arrival at the traps, since adults and older nymphs may have been derived from earlier instars by moulting during the fortnightly exposure period.

In a further experiment, the dispersal of mealybugs to different distances from cacao was studied using a plot of cacao trees with a well-defined edge, to windward of an exposed area of short-cut grass. Buildings and wattle hurdles 10 ft. high along the sides of the plot restricted wind movement across the experimental area (fig. 10). The trees were first heavily infested with *Ps. njalensis* by placing adults in paper cones attached to the branches (*vide* Hanna, Judenko & Heatherington, 1955), and, in October 1955, 294 boxes of ten 2-year-old cacao seedlings were exposed for trapping. These, after first being freed from mealybugs by fumigation, were arranged in a block of 21 rows with 14 boxes in each row; distances between and within rows were four and ten ft., respectively. Three boxes at the end of each row were placed in the cacao, the fourth on the edge of the plot, and the remainder at ten-ft. intervals from the edge. The top rim of each box was grease-banded.

When the seedlings were examined for mealybugs five months later, the pattern of infestation (fig. 10) showed a marked drop in the number of traps supporting *Ps. njalensis* with increasing distance from the cacao, the relationship providing a sigmoid curve. The mean number of traps infested was seven under the cacao, seven at the edge of the plot, six (0.86) at 10 and 20 ft. away, four (0.57) at 30 ft. and one (0.14) at 40 to 100 ft.; the figures in brackets represent

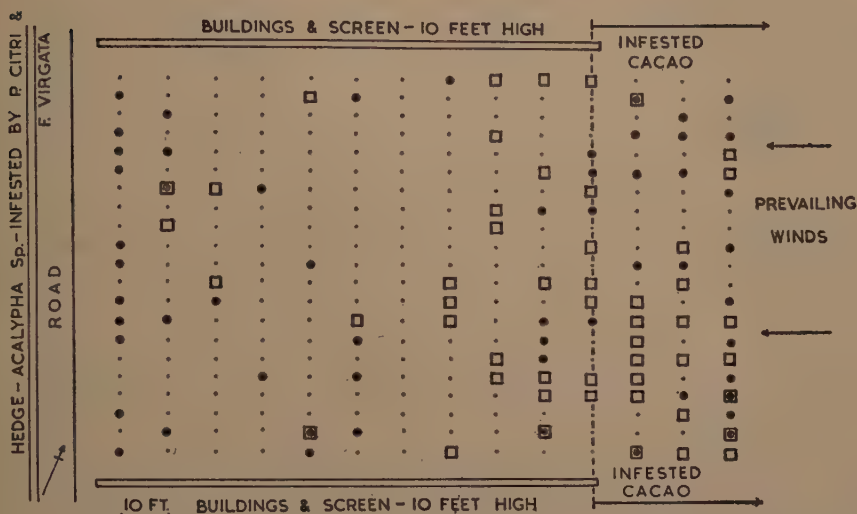


Fig. 10.—Patterns of infestation by *Ps. njalensis*—□, and either *Pl. citri* or *F. virgata*—●, on cacao seedlings exposed to aerial dispersal under infested cacao and at distances from it.

the number of boxes infested as a proportion of those infested under the canopy. The pattern for combined catches of *Pl. citri* and *F. virgata* was somewhat different; the number of traps infested by these species fell considerably at only 20 ft. from the cacao, but there was a high infestation on traps furthest from the trees. It must be presumed that these species spread from the infested hedge of *Acalypha* sp. bordering this end of the plot.

Seasonal changes in aerial dispersal.

Changes in the abundance of windborne mealybugs may be related to changes in air movements, the population of the species, and their mobility on plant hosts. While such factors will affect the numbers of insects caught on sticky and seedling traps, catches on the latter may also be influenced by factors which affect mealybug establishment, viz., ant attendance, insolation and rainfall. The number of variables makes it impossible in this study to relate changes in catch to environmental factors. It is of interest, however, to examine the variations which occurred on the two types of trap in cacao, particularly as regards their relationship with rainfall.

Data for sticky traps were provided by the 'elevation' experiment (Oct. 1954–Apr. 1956), described above, to study aerial movement in cacao. 'Supplementary' data were obtained from 160 sticky traps exposed six ft. above the ground, in pairs, at 80 randomly selected sites in cacao. These traps were examined at fortnightly intervals between December 1954 and April 1955.

Seasonal changes in catch on seedling traps were studied by sowing cacao beans in clearings in mature cacao (Pl. VIII, fig. 2). Five sites were selected, all within a quarter of a mile of each other, at each of which 16 seedbeds ($4' \times 6'$) were prepared and randomly assigned to different planting dates, 250 cacao beans being sown at each site every four weeks. The resulting plants were cut level with the ground and examined eight weeks after sowing; but because

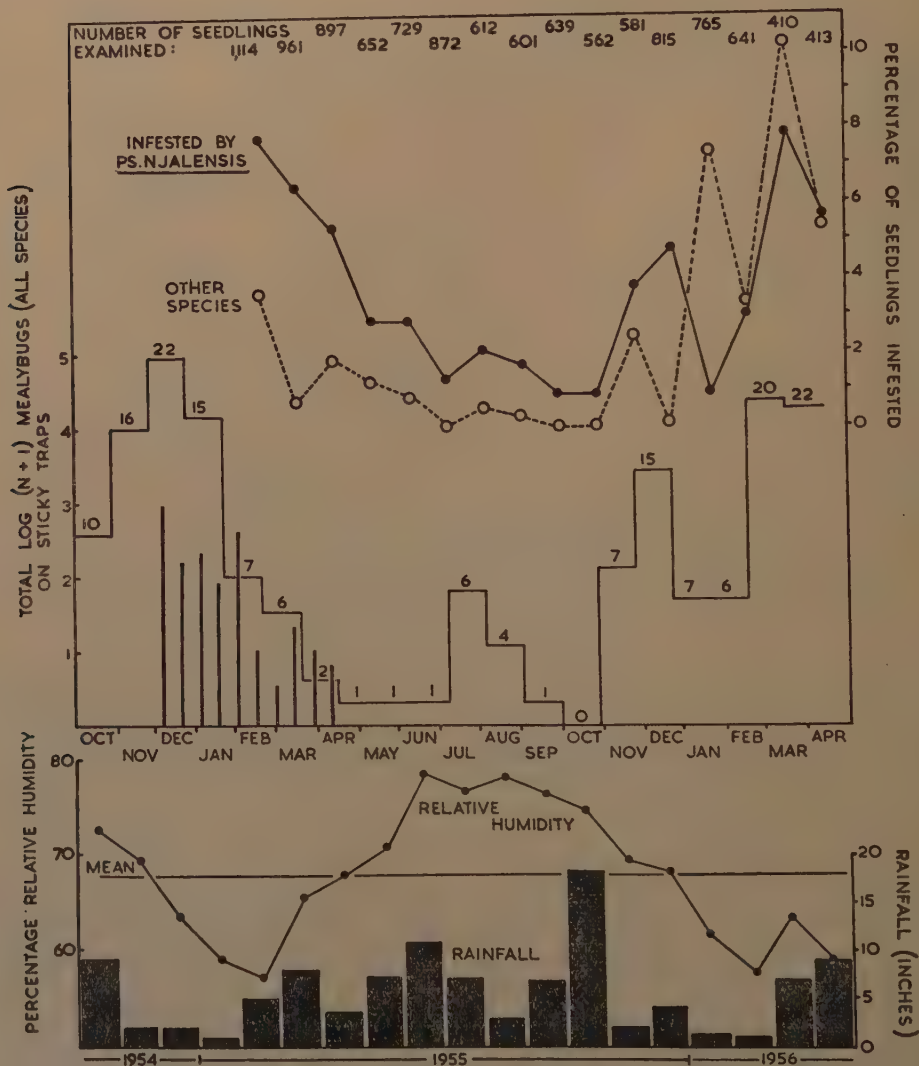


Fig. 11.—Seasonal changes in the catch of airborne mealybugs on sticky traps and on cacao seedlings within farmers' cacao. Upper histograms relate to catches in the 'elevation' experiment (open bars) and 'supplementary' experiment (narrow solid bars)—see text, p. 191. Arithmetic total catches in the 'elevation' experiment are shown for four-weekly trapping periods. Numbers of airborne mealybugs are highest during months of low rainfall and periods of low relative humidity.

the first true leaves are not fully exposed for about four weeks, catches have been related only to the remainder of the growing period (fig. 11). Since the viability of cacao seed is retained for only a few days after the harvesting of pods, and germination can be adversely affected by weather, the number of seedlings successfully raised varied throughout the year. For this reason the percentage of seedlings becoming infested by mealybugs was calculated to provide a measure of aerial dispersal. The relative proportions, in percentages, of seedlings infested by the commoner species were *Ps. njalensis* 65.6, *Pl. citri* 29.1 and *F. virgata* 5.3.

Similar trends in catch were obtained for both sticky and seedling traps (fig. 11). The highest catches on sticky traps (in both 'elevation' and 'supplementary' data) were recorded during December 1954, followed by a marked, progressive drop to a low level in May-June 1955. On seedlings, there was a comparable decline in infestation rate by *Ps. njalensis* and other species. Both types of trap showed a slight rise in catch during July, followed by a minimum in October and peaks in December 1955 and March-April 1956. On seedlings, similar trends were obtained for both *Ps. njalensis* and other species except during December-January 1956, when the infestation rates of the two groups were markedly reversed. The data for rainfall indicate that aerial dispersal occurs more readily during dry conditions, particularly in the main dry season and to a lesser extent in the brief dry period between the first and second rains.

The establishment of airborne mealybugs on cacao.

Insolation, rainfall and ant attendance have been listed above as factors which might affect the establishment of airborne mealybugs on seedling traps; but, in experiments described in the preceding section, it was not possible to control differences in insolation without modifying the effects of rainfall and, it was feared, influencing the chances of mealybugs falling on the plants. The following experiments were carried out to examine the effects of protection from weather on the infestation of seedling traps insulated from ants and of young trees with (*inter alia*) ant attendance encouraged or otherwise.

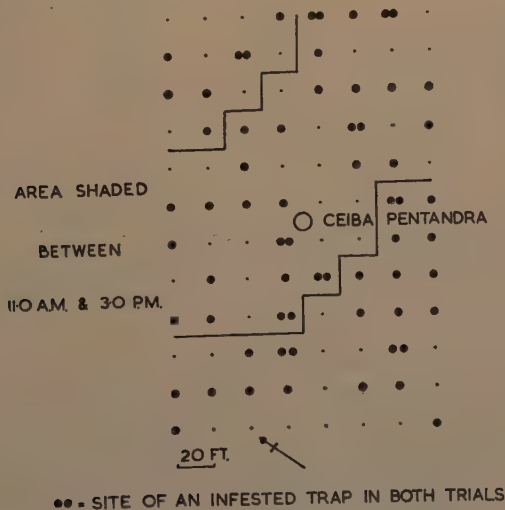


Fig. 12.—Baskets of cacao seedlings infested by *Pl. citri* and *F. virgata* in two trials (black circles) in relation to the distribution of light shade provided by a central tree (*Ceiba pentandra*).

On cacao seedlings.

Ninety-six traps were arranged in a block of 8 × 12 rows, 20 ft. apart, around a central tree of the species *Ceiba pentandra* (Pl. VIII, fig. 3), in such a way that half were shaded by the branches between 11.0 a.m. and 3.0 p.m. daily. These traps consisted of cacao seedlings in large baskets filled with soil and raised three ft. off the ground on supports smeared with banding grease. Twenty-five cacao beans were sown in each basket and the developing seedlings thinned to 20 after germination. The experimental area supported short-cut grass and the distance of traps from the nearest cacao was 200 ft.

Two preliminary trials were carried out, in which the seedlings were examined for mealybugs eight weeks after planting. The pattern of infestation for the two trials combined, and the area lightly shaded by the tree between 11.0 a.m. and 3.0 p.m., are shown in fig. 12. The numbers of traps infested in the exposed and shaded areas were 31 and 33, respectively.

To increase the density of shade and to provide greater protection from rainfall, palm fronds and plantain leaves were supported 8 ft. above the ground over alternate traps in each row. Considering the preliminary experiments as 'uniformity trials' there was found to be no significant difference between the infestation rates of traps which constituted the two treatments (Table V). Two

TABLE V.

The effect of artificial shade and protection from rainfall on the establishment of airborne mealybugs on cacao seedlings.

Trials	Percentage of traps infested by mealybugs			
	Uniformity trials (before the erection of artificial shade)		After the erection of artificial shade	
	A	B	Shade A	No shade B
1st	18.8	22.9	41.7	18.8
2nd	43.8	47.9	41.7	33.3
Means	33.3	35.4	41.7	26.0

further trials were carried out, using the artificial shade; these showed a significant increase ($P < 1\%$) in the numbers of traps infested under shade, despite the palm and plantain leaves possibly preventing some airborne mealybugs from reaching the seedlings. The majority of traps became infested by *Pl. citri* and *F. virgata*; none supported *Ps. njalensis*.

On cacao trees.

A final experiment was carried out to examine the factors which affect mealybug establishment on young cacao trees. These included the presence or absence of attendant ants, artificial shade (heavy) *versus* existing shade (light), and a comparison of mealybug establishment following natural dispersal and when assisted by artificial colonisation. This study was made in the W.A.C.R.I. 'Thinning Trial' using eight-year-old Amelonado cacao, 10 ft. apart, after the *Gliricidia* shade trees had been coppiced.

In each of eight 100-tree plots, 16 experimental trees, 6-8 ft. high, were selected for ease of examination and absence of mealybugs; in no instance were

they adjacent, either in the rows or diagonally, or in contact with neighbouring trees. All ant nests on the cacao were removed. Eight trees per plot, selected at random, were shaded by canopies of palm and plantain fronds on supports 8-10 ft. high. Half the shaded and unshaded trees then had pieces of dead wood harbouring nests of the ant, *Crematogaster striatula* Emery, tied to their trunks, and half the trees in each of these four treatments were artificially colonised with 100 adults of *Ps. njalensis* in groups of 25, placed in four paper cones attached to the branches. A laboratory test showed that 100 adults can produce about 1,000 first-instar nymphs in six days.

Colonisation with mealybugs and attachment of ant nests were carried out simultaneously between 2nd and 10th May 1955; vacated nests were replaced a week later on 31 trees, again on 3rd June on 28, and finally on 20th June on 25. Some nests still failed to establish themselves because of competition with resident ants of other species, and these nests were not replaced further. All experimental trees were examined for established colonies of mealybugs on 6th June, 18th August and 10th October, when records were also made of ant species present.

The percentage of trees infested for each treatment is shown in Table VI. After transforming percentages to angles, an analysis of variance showed that the higher infestation rates under artificial shade and where ant nests had been introduced were not significant. Twice as many trees supported established colonies of mealybugs after artificial colonisation ($P < 5\%$), than when the development of an infestation was left to natural dispersal alone.

TABLE VI.

Percentages of cacao trees supporting colonies of *Ps. njalensis*, under normal or dense artificial shade, as a result of natural or artificially augmented infestation, with or without attempts to establish *Crematogaster* ants.

Artificial shade	Present		Absent		Mean
	with	without	with	without	
With or without attempts to establish nests of <i>C. striatula</i>					
Infestation from natural dispersal alone	31.3	12.5	25.0	18.8	21.9 ($P < 5\%$)
This augmented by 100 adults of <i>Ps. njalensis</i> /tree	62.5	31.3	37.5	31.3	40.7
Means	46.9	21.9 34.4	31.3	25.1 28.2	

The absence of established colonies on 60 per cent. of trees following artificial inoculation with large numbers of mealybugs requires explanation. This figure is very similar to the one of 63 per cent. for cacao trees found completely free from mealybugs during a previous survey in the same area (Cornwell, 1957). It is partly explained by the association of different ant genera with the infested and uninfested trees (Table VII). Using the chi-squared test, there was found to be a highly significant relationship ($P < 0.1\%$) between the presence or absence of infestation (irrespective of its source) and the established ant group. Although the class frequencies for infested trees were too small for a statistical appraisal of the association between ant genera present and the manner of mealybug infestation, there was striking agreement for the two methods; analysis for the uninfested trees showed no evidence of heterogeneity. The close association of

TABLE VII.

Numbers of trees infested by *Ps. nivalensis* or free from mealybugs as a result of natural dispersal alone or artificially augmented, in relation to the presence of different ant genera.

Mealybug infestation		Present			Absent	
Method of infestation		Natural dispersal alone	Augmented by artificial colonisation	Total	Natural dispersal alone	Augmented by artificial colonisation
Ant genera present	<i>Crematogaster</i> , or <i>Pheidole</i> , or <i>Camponotus</i>	14	23	37	30	22
	<i>Oecophylla</i> , <i>Macromischoides</i> , or none	0	3	3	20	16
Not tested					0.07, $P = 50 - 90\%$	
					14.52, $P < 0.1\%$	
					Total	
					52	
					36	

Crematogasterine ants with high mealybug populations on cacao is already firmly established (Strickland, 1951; Cornwell, *op. cit.*). From the results of the present study it may be concluded that the presence of mealybug-attending ants is almost essential for infestations of *Ps. njalensis* to develop, but their absence is not the only factor limiting successful establishment, since these ants were recorded on 52 of 88 trees that remained uninfested, and only 37 out of 89 trees on which they were recorded (*i.e.*, 58%) became infested.

Discussion.

Factors responsible for the spread of cacao viruses have been reviewed by Thresh (1958). Voluntary movement of vectors through the canopy and their dissemination by air currents are considered primarily responsible for the spread of swollen-shoot disease. The former method of dispersal, examined in an earlier paper (Cornwell, 1958), probably accounts for spread of the viruses over limited distances, from infected trees to adjacent healthy contacts. A study of the second method (Strickland, 1950) showed that Pseudococcids are readily dispersed by air currents in Ghana, particularly during dry periods, and that airborne mealybugs may be trapped at considerable distances from cacao at topographical elevations ranging from 700 to 2,100 ft. above sea level.

In the present study, laboratory tests showed that winds of average speed are unlikely to remove mealybugs from their plant hosts by direct action. Nymphs of certain species, particularly *Pl. citri*, may be easily dislodged, when mobile on cacao trees, by the indirect effect of wind causing branches to shake and scrape together. Traps at different elevations within farmers' cacao indicated that mealybugs tend to fall from the branches and are laterally dispersed below the canopy, near ground level, in the zone of maximum air movement. The distance of dispersal within cacao is usually limited by very low wind speeds; the number of mealybugs on traps, 10–15 ft. from cacao, in small clearings averaged only about 13 per cent. of those caught under a closed canopy of cacao trees. In a larger clearing, 100 ft. across, a distance of 45 ft. from surrounding cacao did not prevent seedlings from becoming infested. Outside cacao, average wind speeds are 10 to 20 times greater and were shown to carry mealybugs at least 100 yd.

This investigation has confirmed the opinion that airborne mealybugs are more abundant during dry conditions. The largest catches were obtained during the dry season (December–February) when maximum temperatures average 91–94°F. The smallest catches were obtained during the cooler wet season (September–October) when this mean falls below 90°F. During both periods, however, mealybug populations on cacao, in areas of high infestation rate, may average 100–200 per tree (Cornwell, 1957); moreover, seasonal changes in wind speed are not sufficiently marked to account for this variation in the trapping data. The evidence suggests that changes in the abundance of airborne mealybugs may be attributable to differences in temperature; high temperatures have been shown to induce the young nymphs to leave the carton coverings which protect the parent colonies (Cornwell, 1958), and the present studies have shown that wind speed is maximal during the afternoon, when the mobility of mealybugs is most pronounced. Because of their small size and absence of wings, mealybugs falling from the branches behave as inert particles becoming readily dispersed in dry air.

The present work has demonstrated that at least eight species of Pseudococcids are carried by air currents, these being *Ps. njalensis*, *Pl. citri*, *Pl. celtis*, *Ps. comstocki*, *Pl. kenyae*, *Ps. hargreavesi*, *D. brevipes* and *F. virgata*, all of which can transmit one or more cacao viruses. The extent to which different species are dispersed in the air can be determined only by live-trapping and rearing insects individually to the adult stage for identification. Certainly, from the experiments on the reservoir, it would appear that *Pl. citri* may become windborne more

readily than other species. It was shown, however, that *Ps. njalensis* is largely dependent for successful establishment on the presence of attendant ants and rarely becomes established in the absence of shade. Thus, the relative abundance of species on seedling traps may largely reflect differences in environmental adaptation.

The extent to which different instars are dispersed by air currents is not accurately known, though it appears reasonably certain that the aerial population is composed of developmental stages in similar proportions to those which comprise the mobile population on plant hosts. However, older instars may fall from the branches more readily than first-instar nymphs so that the average age of the aerial population may be slightly older than that of the mobile population on cacao. This has not been substantiated by trapping because of difficulty in detecting first-instar nymphs on sticky traps, and because of the continued development of nymphs on seedling traps which can be examined only at intervals.

This study has confirmed the opinion that mealybugs dispersed by air currents are capable of establishing themselves and feeding on cacao. Yet there is no experimental evidence which demonstrates conclusively that mealybugs of vector species, when dispersed by wind, are capable of transmitting cacao viruses. Of the 3,000 seedlings exposed to mealybug aerial dispersal on the reservoir, not one developed swollen-shoot disease, although they were retained and examined for virus symptoms six months after completion of the experiment. Nevertheless, field observations indicate similarities in the pattern of virus spread and this type of vector dispersal. The time spent by vectors in being blown from one host-plant to another may be no more than a few seconds, and such short periods would in no way reduce the efficiency of virus transmission (Lister, 1953; Posnette & Robertson, 1950). This being so, vectors dispersed by air currents within cacao would be expected to supplement those moving between the trees by way of canopy branches in contributing to the extension of infection by radial spread, besides causing 'jump spread' over, at least, limited distances.

It is important to mention that radial spread from an established outbreak is rarely uniform in all directions and normally assumes an amoeboid pattern. This might be caused by a variety of factors, *e.g.*, differences in the growth habit of trees influencing canopy movement of vectors, certain wind directions being predominant, or differences in the period of latent infection masking the actual extent of infection at any time. It could also be brought about by differences in the suitability of surrounding trees for mealybug establishment. For example, a single infective mealybug might be blown or walk on to a tree devoid of mealybugs because of the distribution of ant species; it might feed and transmit a virus but still fail to establish a colony. Further spread from such a tree is unlikely until it does support an established population. On the other hand, an infective mealybug may be blown on to a tree already infested by Pseudococcids and coccidophilic ants, or it may give rise to such infestation. After a suitable period for virus multiplication, the rate of spread from this tree is likely to be considerable. Thus, in Ghana, where the dominant vector species on cacao is *Ps. njalensis*, the distribution of ant species might contribute substantially to the amoeboid pattern characteristic of swollen-shoot outbreaks.

Aerial movement of vectors is considered responsible for the formation of 'satellite' outbreaks of swollen-shoot disease. The proven wind dispersal of mealybugs from one host-plant to another over distances exceeding 100 yd. substantiates this suggestion. Whilst there is no experimental information on the effects of the gale-force winds experienced at the end of the dry season, the writer is of the opinion that these may carry mealybugs to high altitudes and disperse them speedily over many miles. Observation of the movement of 'silk cotton' (the contents of the fruits of *Cecropia pentandra*) during these winds certainly gives evidence of their dispersive power. The distance of 'jump spread' from

an existing infection is usually only a few yards, but not infrequently new outbreaks develop in areas which are otherwise completely free from the disease. The extent to which the wild hosts of cacao viruses contribute mealybugs to the aerial population is unknown, but it must be noted that vectors on forest trees may be of considerable importance in the process of long-distance 'jump spread' since they may be subject to wind speeds far in excess of those experienced in the cacao itself. In this connection, Pseudococcid species other than *Ps. njalensis* may play a large part in spreading infection. Clearly, *Pl. citri* may be more important in 'jump spread' than mere numbers would suggest, since this species may be more readily windborne or may more easily establish itself on cacao.

It is difficult to visualise methods which could be adopted to prevent virus spread by airborne vectors. There is little doubt that wider spacing of the crop, which might reduce mealybug migration through the canopy, would tend to increase wind speeds in the cacao and encourage aerial dispersal. As for the retention of a closed canopy and the interplanting of a barrier crop, suggested as the most suitable method of reducing spread by way of the canopy (Cornwell, 1958), it is doubtful whether any economic crop could be found to produce sufficient intercepting foliage in the canopy and near ground-level, where most lateral dispersal occurs.

Strickland (1950) suggested that virus spread by airborne Coccids might be prevented by the large-scale use of insecticidal sprays and dusts during the dry season. In cacao with a closed canopy, 72 per cent. of airborne mealybugs were trapped at heights below 14 ft. Thus, spraying the trunks with contact insecticides merits consideration, particularly as this might prevent the build-up of vector populations on pods (cacao is largely cauliflorous, Pl. VII, fig. 2) during the crop season. Moreover, such treatment could be combined with measures of ant control, should research in this field (Taylor, 1958; Entwistle, 1959) lead to a practical method of indirectly controlling the major vector, *Ps. njalensis*, and thereby reducing virus spread in cacao.

Summary.

The aerial dispersal of the Pseudococcid vectors of virus diseases of cacao in Ghana and the possible influence on it of wind speed was studied at Tafo. Seasonal variations in wind speed in Ghana are slight, particularly inland in the cacao-growing areas. Observations at Tafo during 1955 showed that air movement was maximal between 12.30 and 3.0 p.m. and minimal during the hours of darkness. Daily wind speeds in the open, from April to November 1955, averaged 1.1 m.p.h., 4 ft. above ground. About 80 per cent. of wind speeds measured in one-minute periods on two days in February 1955 were within the range 1-5 m.p.h. and 11-12 per cent. between 5 and the maximum recorded speed of 7 m.p.h.

In cacao, wind speed is reduced by a factor of 10-20 times; daily speeds averaged 0.09 m.p.h. at 8 ft. above ground during April and May 1955. The highest daily averages under a closed canopy (400-650 ft./hr.) were recorded 2 ft. above ground-level; speeds fell to a minimum (25-125 ft./hr.) in the canopy at 15-25 ft., and rose again above the canopy at 30 ft. to a speed (250-350 ft./hr.) comparable with that just below the branches at 10 ft. At breaks in the canopy caused by the removal of diseased trees, daily averages were lowest (125-150 ft./hr.) 2 ft. above the ground. They rose to a peak (400-600 ft.) on a level with the lower branches of the canopy, dropped markedly (250-450 ft./hr.) at the level of the middle canopy and rose to a maximum (650-1,000 ft./hr.) at 30 ft.

All instars of *Pseudococcus njalensis* Laing walking on pieces of cacao wood in the laboratory withstood removal at air speeds of 10 m.p.h., but these and corresponding stages of three other species could be dislodged by gently tapping the wood. The late nymphs and adults of *Ps. njalensis* and *Ps. gahani* Green

were more easily removed than their 'crawlers', though this difference was not found between the developmental stages in *Planococcus citri* (Risso) and *Ferrisia virgata* (Ckll.). Amongst the four species tested, first-instar nymphs of *Pl. citri* were most easily dislodged, and those of *Ps. njalensis* or *F. virgata* more so than those of *Ps. gahani*.

Airborne mealybugs were caught on adhesive traps, on bait twigs pinned to mature trees, and on cacao seedlings. Eight vector species became established on cacao after dispersal by air currents.

Under a closed canopy, more airborne mealybugs were caught at two and ten feet above ground than at levels in and above the canopy. At breaks in the canopy, catches averaged about 13 per cent. of those obtained under a continuous canopy and were insufficient to show changes in aerial density with height. The distribution of catches over the surface of traps would suggest that mealybugs drop from the branches, are carried by air currents when falling, and become laterally dispersed at levels a few feet above the ground.

In a clearing where cacao had been removed to simulate conditions following the routine cutting out of virus-infected trees, airborne mealybugs became established on seedlings at a distance of 45 ft. from infested cacao trees. The ratios of boxes of seedlings which became infested by aerially dispersed *Ps. njalensis* at increasing distances from infested standing cacao, in relation to those beneath it (unity), were: 0.86 at 10–20 ft., 0.57 at 30 ft. and 0.14 at 40–100 ft. Under conditions of high insolation, the maximum recorded distance of mealybug aerial dispersal from surrounding vegetation to cacao seedlings was 340 ft. Aerial catches on seedlings 40 to 165 ft. from cacao showed an over-all decrease with distance.

Aerial dispersal is more pronounced during dry conditions, particularly during the main dry season, December–February, and to a lesser extent during the brief dry period experienced in July or August.

The infestation rate of cacao seedlings by windborne mealybugs (predominantly *Pl. citri* and *F. virgata*) was increased by 50 per cent. when plants were protected from weather by artificial shade. These traps, insulated from ants, failed to become infested by *Ps. njalensis*.

Out of 64 young cacao trees, 22 per cent. became infested by airborne vectors during the five-month period May to September 1955; when, for similar trees, normal dispersal was augmented by an initial artificial colonisation with *Ps. njalensis*, the corresponding figure was 41 per cent. The infestation rate, after either augmented or natural dispersal, was not significantly affected by attempts to establish on the trees nests of the ant, *Crematogaster striatula* Emery, or by affording protection from the weather in the form of artificial shade. It was evident, however, that the presence of mealybug-attending ants is almost essential for infestations of *Ps. njalensis* to develop, but there must be other limiting factors, since establishment failed on 58 per cent. of trees on which coccidophilic species were present.

The part played by airborne vectors in extending infection by radial and 'jump spread' is discussed, together with the possible use of insecticidal measures to prevent their establishment on the trunks of healthy cacao.

References.

- CORNWELL, P. B. (1956). Some aspects of mealybug behaviour in relation to the efficiency of measures for the control of virus diseases of cacao in the Gold Coast.—*Bull. ent. Res.* **47** pp. 137–166.

- CORNWELL, P. B. (1957). An investigation into the effect of cultural conditions on populations of the vectors of virus diseases of cacao in Ghana with an evaluation of seasonal population trends.—*Bull. ent. Res.* **48** pp. 375–396.
- CORNWELL, P. B. (1958). Movements of the vectors of virus diseases of cacao in Ghana. I. Canopy movement in and between trees.—*Bull. ent. Res.* **49** pp. 613–630.
- ENTWISTLE, P. F. (1959). Mealybug studies.—*Rep. W. Afr. Cocoa Res. Inst.* 1957–58 pp. 31–36.
- HANNA, A. D., JUDENKO, E. & HEATHERINGTON, W. (1955). Systemic insecticides for the control of insects transmitting swollen-shoot virus disease of cacao in the Gold Coast.—*Bull. ent. Res.* **46** pp. 669–710.
- LISTER, R. M. (1953). Persistence of virus in starved vector.—*Rep. W. Afr. Cocoa Res. Inst.* 1952–53 p. 9.
- POSNETTE, A. F. & ROBERTSON, N. F. (1950). Virus diseases of cacao in West Africa. VI. Vector investigations.—*Ann. appl. Biol.* **37** pp. 363–377.
- STRICKLAND, A. H. (1947). Coccids attacking cacao (*Theobroma cacao*, L.), in West Africa, with descriptions of five new species.—*Bull. ent. Res.* **38** pp. 497–523.
- STRICKLAND, A. H. (1950). The dispersal of Pseudococcidae (Homoptera-Hemiptera) by air currents in the Gold Coast.—*Proc. R. ent. Soc. Lond.* (A) **25** pp. 1–9.
- STRICKLAND, A. H. (1951). The entomology of swollen shoot of cacao. II. The bionomics and ecology of the species involved.—*Bull. ent. Res.* **42** pp. 65–103.
- TAYLOR, D. J. (1958). Effect of dieldrin on ant activity.—*Rep. W. Afr. Cocoa Res. Inst.* 1956–57 pp. 37–39.
- THRESH, J. M. (1958). The spread of virus disease in cacao.—*Tech. Bull. W. Afr. Cocoa Res. Inst.* no. 5, 36 pp.
- WALKER, H. O. (1957). Surface wind frequencies.—*Dep. Note Ghana met. Dep.* no. 7.
- WILLIAMS, D. J. (1958). The mealy-bugs (Pseudococcidae: Homoptera) described by W. J. Hall, F. Laing and A. H. Strickland from the Ethiopian Region.—*Bull. Brit. Mus. (nat. Hist.) Ent.* **7** pp. 1–37.

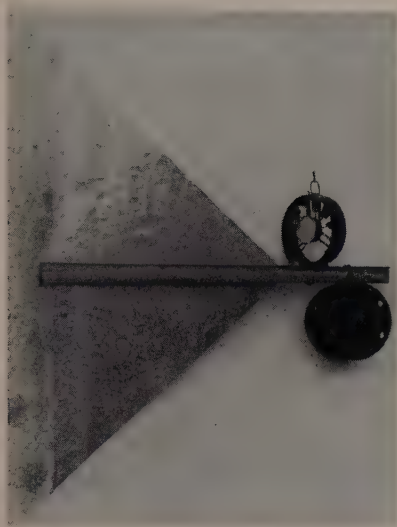


FIG. 1. Vane anemometer modified for field use.



FIG. 2. Farmers' cacao with closed, interlocking canopy and complete absence of ground vegetation.



FIG. 3. Sticky traps erected at an open canopy site; arrows indicate surrounding foliage of cacao canopy.



FIG. 4. Sticky traps at 2ft. above ground showing 'top', 'side' and 'bottom' trapping surfaces.



FIG. 1. Seedling traps on W.A.C.R.I. reservoir at different distances from cacao.



FIG. 2. A seedling plot, eight weeks old, sown to examine seasonal changes in mealybug infestation rate.



FIG. 3. Layout of seedling traps (in baskets) to examine the effects of shade from a central specimen of *Ceiba pentandra* on the establishment of airborne mealybugs.

INSECT INFESTATION OF STORED RAW COCOA IN GHANA.

By J. E. CRANHAM *

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Measures for the control of insects infesting stored raw cocoa were adopted by the Ghana Cocoa Marketing Board in April-May 1956, together with the first extensive survey of infestation in Ghana cocoa. The author was employed from April 1957 to June 1958 by Messrs. Pest Destruction (West Africa) Ltd., the contracted agents of the Marketing Board, to investigate the efficacy of certain control measures and the origins and development of infestation. The control measures adopted † involved the use of a formulation of synergised pyrethrin in white oil applied within storage sheds as a finely dispersed spray ('fogging'), from which a film was deposited on the surfaces of stacked bags of cocoa ('film-spraying'). Spraying was commenced in the ports and in the largest up-country centres in 1956-57, and in the 1957-58 cocoa main-crop season it was extended temporarily to cover most of the up-country centres. Fumigation with methyl bromide, under gas-proof sheets, had also been recommended and was used in 1957-58 for the treatment of more heavily infested cocoa.

'Main-crop' cocoa (about 200,000-250,000 tons) is harvested from September to December, and after fermentation and drying is normally passed quite rapidly from the many thousands of small farmers to brokers or middlemen who sell to, or act on behalf of, the various licensed buying agents of the Marketing Board. The cocoa is graded at nearly 400 centres by the Produce Inspection Department of the Ministry of Trade and Labour, and after grading is 'sealed' in hessian sacks of 140 lb. gross weight. The small metal seal bears on one side a number indicating the month of sealing ('seal number'), and on the other side the number of the Produce Examiner concerned. The bag itself bears stencil marks indicating the grade and point of origin ('station mark'). Cocoa is transported to the ports and shipped, when possible, in order of seal number. A considerable part of the main crop may be stored in Ghana for six months or more, some up to nine months, principally in licensed sheds in the larger up-country centres and the ports. The very small 'mid-crop', which is usually purchased in June and July, is shipped more rapidly.

In the assessment of pest infestation, extensive use has been made of the technique of sieving or 'screening' whole bags of cocoa to determine insects free in the bag, *i.e.*, not inside cocoa beans. This method, and a design of sieve, were recommended by D. W. Hall (Dep. Sci. industr. Res., 1958, p. 48). A large rectangular sloping sieve of 1/5 in. mesh is used, standing on four legs and having an enclosed removable tray beneath. Each bag of cocoa is emptied slowly at the top and moved by hand down the sieve, so that free insects (together with some cocoa fragments and débris) fall through to the tray where they can be counted. This method is a great improvement on the 'snaking' of bags, used previously and mentioned by Cotterell (1952). Examination of beans taken by 'spear-sampling', as in the grading of cocoa, was also used for assessing insect damage and insects inside the beans ('grading' assessment). Visual observations of adult moths and beetles active in the cocoa sheds were also useful, but no

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† As recommended by a United Kingdom Advisory Committee, through Dr. D. W. Hall, Tropical Liaison Officer, Pest Infestation Laboratory, Slough.

attempt was made to estimate the numbers by trapping. Riley (1957) has shown that the relative abundance of different species of insects active around the stacks bears no relation to the relative abundance of species in the cocoa.

There is a dearth of published data on insect infestation in stored cocoa. Cotterell (1934) described the infestation of beans in the Gold Coast by *Araccerus fasciculatus* (Deg.) and *Ephestia cautella* (Wlk.), and later (1952), recorded the decline in numbers of *Araccerus* following better drying of cocoa, and the increasing occurrence of *Lasioderma serricorne* (L.) in Western Nigeria. Riley (1957) studied the build-up of infestation in a single stack of bagged cocoa in Western Nigeria, assessing infestation by spear-sampling of beans and trapping adult insects with sticky traps.

The present paper deals with the data obtained by sieving and grading assessment, together with observations on the origins of infestation and the build-up during storage. Data on the climatic conditions in cocoa sheds, in relation to the effect on infestation and control measures, are also presented. The organisation and practice of spraying or fumigation are not described, but evidence obtained on the effect and potential value of spraying is discussed.

ASSESSMENT OF INSECT INFESTATION.

Sieving.

Assessment of infestation in cocoa by sieving was initiated by the Ghana Produce Inspection Department in February 1956, being carried out at the ports, with the object of controlling the export of heavily infested cocoa.

In the 1957-58 main-crop season, sieving was extended to cover cocoa prior to railing at five Ashanti railheads. These centres—Kumasi, Ejisu, Bomfa, Konongo and Bekwai—rail to the port of Takoradi over four-fifths of the Ashanti crop. This extension had the practical object of selecting more heavily infested cocoa for fumigation at Takoradi, but it also yielded some useful data on infestation.

At the beginning of the 1957-58 season, ten 'insect counters' attached to the Produce Inspection Department were trained as special staff by the author for work at the ports, and six men were trained for Kumasi; they carried out all sieving and counting at the ports and Kumasi. In Ejisu, Bomfa, Konongo and Bekwai, the lesser amount of sieving involved was carried out by Produce Examiners and Supervisors.

Many bags were also sieved personally, particularly in Ashanti, for the purpose of more precise investigation and as a check on the validity of the counts made by Produce Inspection Department.

Species of insects occurring.

In 1957-58, only the following species of insect pests occurred frequently and in more than odd ones and twos: *L. serricorne*, *E. cautella*, *A. fasciculatus*, *Tribolium castaneum* (Hbst.), *Carpophilus dimidiatus* (F.), *Cryptolestes* spp., *Ahasverus advena* (Waltl), and an unidentified species of Silvanid.

Larvae of all of these species except *A. fasciculatus* were also present in the sievings; they occurred in smaller numbers than did the adult insects, except in the case of *Tribolium* and *Lasioderma* from May onwards, in Kumasi.

It would appear that a wider range of stored-product beetles strays into cocoa in very small numbers but that only the above species can breed and increase to any extent; *Cryptophagus* sp., *Gnathocerus maxillosus* (F.), and an unidentified species of Tenebrionid develop in small numbers occasionally.

Other species found on cocoa coming into storage, but very seldom during storage, include *Calandra oryzae* (L.), *Oryzaephilus surinamensis* (L.), *Palorus subdepressus* (Woll.), *Necrobia rufipes* (Deg.) and *Tenebroides mauritanicus* (L.).

Psocids occurred frequently in small numbers, and occasionally in large numbers (when the moisture content was high) but mites, predacious Anthocorids and spiders were few in numbers in the season. Hymenopterous parasites, at present unidentified, occurred in small numbers, occasionally becoming more abundant; fair numbers were seen at Ejisu in association with a heavy incidence of *Ephestia cautella*.

Results in Ashanti.

From each vanload of cocoa (320–400 bags), four bags were taken and sieved by Produce Inspection staff. The count was divided into three categories of insect species: (1) *L. serricornis*, (2) *E. cautella* and *Araecerus fasciculatus* together, (3) adults of other beetles, including *Tribolium castaneum*. These categories had been used previously by Produce Inspection staff, who recognised them easily, and it was not practicable to have more than three categories for them to count. Larvae, except those of *Ephestia*, were not included in the count, because most could not be seen amongst the cocoa fragments and general debris on the counting tray. *Ephestia* larvae and pupae were counted, it being chiefly the immature stages of this species that are found inside the bag. Other arthropods were not counted.

Staff made a daily return on all cocoa sieved prior to railment, covering over 17,000 bags sieved between October 1957 and June 1958. From these data were computed monthly averages of insects per bag for each category, and the percentage of bags infested, that is, showing any insects at all. Although counts were often underestimates of the true numbers present, the data thus obtained, in combination with personal observations and the sieving of 339 bags, allow certain valid conclusions to be drawn, and these are detailed in the subsections that follow.

(1) The initial infestation on cocoa coming into licensed storage at the beginning of the season was very light but included all the common species and about half the bags examined were found to be infested. Table I gives the data on bags examined in Kumasi in September and October.

In cocoa railed in October, November and December, after short periods of storage, the infestation averaged only 1–2 insects per bag, although affecting about half the bags. Approximately 40 per cent. of the bags contained 'other

TABLE I.

Insects sieved from cocoa coming into licensed storage early in the season. Kumasi, 1957.

Species	Average number of insects per bag	
	September (93 bags)	October (36 bags)
<i>Lasioderma serricornis</i> ..	0.07	0.11
<i>Ephestia cautella</i> ..	0.01	0.03
<i>Araecerus fasciculatus</i> ..	0.02	0.00
<i>Tribolium castaneum</i> ..	0.29	0.18
<i>Cryptolestes</i> spp. ..	0.06	0.12
<i>Ahasverus advena</i> ..	0.31	0.52
<i>Carpophilus dimidiatus</i> ..	0.02	0.03
A species of Silvanid ..	0.39	0.28
Other spp. ..	0.46	0.30
Total (all species) ..	1.63	1.57

beetles' but *Lasioderma*, and *Araccerus* and/or *Ephestia* occurred in about 10 per cent. of the bags. Up to the end of December 1957, only 22 out of 8,038 bags sieved yielded more than 10 insects per bag, and only nine bags exceeded 20 per bag. Thus the infestation at the beginning of the season was uniformly of a low order but was present in a fairly high proportion of the bags at all centres.

(2) The monthly average infestation recorded in cocoa railed, month by month, from Kumasi, and from the four other Ashanti centres taken together, is shown in fig. 1. The monthly average numbers of insects per bag, for the three categories separately and for the total of all species, are plotted as $\log(n+1)$ values. These figures show in effect the general increase in infestation with increasing storage period. The figures relate, of course, to cocoa as it was railed by seal number (see p. 203).

The cocoa main crop is harvested from September to December and the bulk of the crop (up to 90%) is sealed before the end of January. October, November, December and January are the four months of heavy grading and sealing. Most cocoa is graded and sealed soon after preparation, but a small minority is retained unsealed by the brokers and sometimes by licensed buying agents until February, March or even April. Cocoa sealed in these later months, therefore, probably has had a longer storage period than is suggested at any time by the seal number.

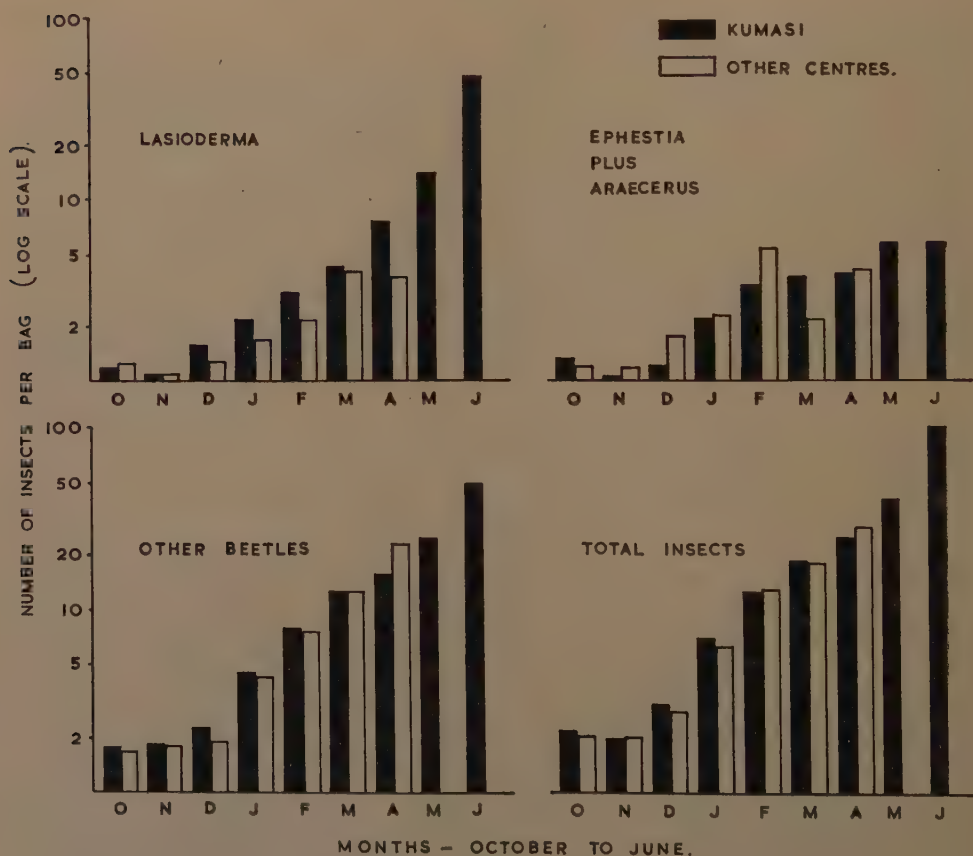


Fig. 1.—The increase in infestation in bagged cocoa during storage in Kumasi (from October 1957 to June 1958) and in other Ashanti centres (from October 1957 to April 1958). Assessment by sieving.

It will be seen from Table II that each seal of cocoa shows a month-by-month increase in infestation, given here as average total numbers per bag. Up to and including March, the 'oldest' seal has the highest infestation, but in April the

TABLE II.

Development of infestation in different 'seals' of cocoa.

Month of sealing	Average number of insects per bag at time of railing in 1958				
	January	February	March	April	May
1957 November ..	8.6	N	N	N	N
December ..	5.6	15.4	22.0	16.2	N
1958 January ..	3.1	8.3	16.3	25.8	46.0
February ..	N	3.4	12.6	23.2	36.0
March ..	N	N	N	N	46.2
April ..	N	N	N	N	78.0

N = not railed.

infestation was fairly even. The movement and shipping of cocoa in order of seal number is therefore of value until April, from when onwards the different seals have, on average, a similar degree of infestation. This has been confirmed by sieving personally in the ports in April and May.

Thus, in considering the data from which the histograms in fig. 1 are plotted, we may be certain that the bulk of the cocoa sieved in Ashanti in January had been in store for at least 1-2 months, in February for 2-3 months, and in March for 3-4 months, and so on. The rate of increase in numbers of the different species will be considered later, in conjunction with the results of personal sievings.

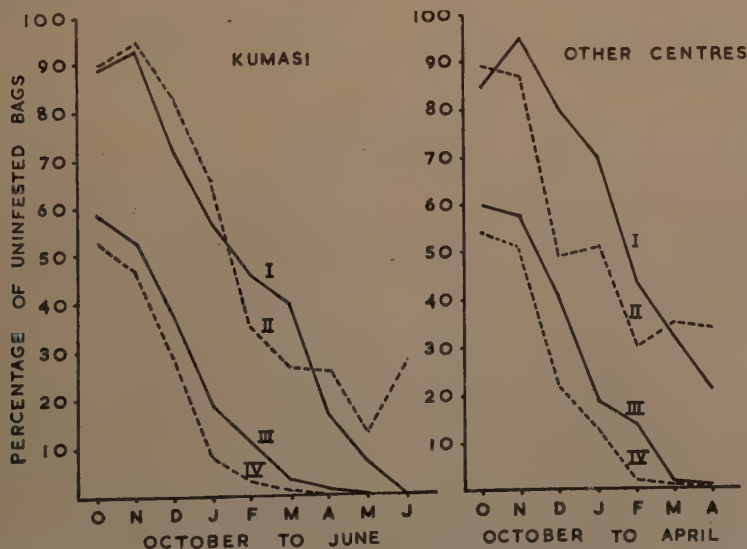


Fig. 2.—The proportion of bags free from (I) *Lasioderma serricorne*, (II) *Ephestia cautella* and *Araecerus fasciculatus*, (III) other species of beetles, and (IV) any species of insect, during storage in 1957-58 in Kumasi (left) and other Ashanti centres (right) as determined by sieving.

(3) The percentage of bags found free from infestation on sieving decreased steadily with increasing period of storage. The percentages of bags sieved each month that did not contain (I) *L. serricorne*, (II) *Ephestia* or *Araecerus*, (III) other beetles, (IV) any species of insect, are shown in fig. 2 for Kumasi and for the other Ashanti railheads.

It is not known how far the increasing proportion of bags infested is a measure of bag-to-bag cross-infestation, or is due to the development to the adult stage of an infestation in the beans at the beginning of storage. The former certainly occurs to some extent, since adults of most species frequently leave the bags inside a stack. In any event, it is apparent that the general increase in infestation involves the vast majority of bags from all districts.

(4) Comparison of the counts from the five Ashanti railheads at which regular sieving was carried out shows that the initial infestation and its subsequent build-up was of the same order at each. For the sake of brevity, the data on all five centres are combined. In figs. 1 and 2, Kumasi is shown separately, and the other four centres taken together (see below).

These five centres between them rail cocoa from most of the districts of Ashanti; there was no evidence of some of these districts being sources of heavier infestation than others. It is fairly certain, however, that there are differences between Ashanti, as a whole, and the Eastern Region, particularly the Oda-Swedru-Winneba area. The same conclusion was reached from a study of degree of infestation in relation to 'station marks' on the cocoa bags; these marks indicate where the cocoa was purchased. In fact, no repeated high infestation was found at all in Ashanti cocoa up to the end of December 1957.

(5) All sheds were sprayed twice weekly, at 3-4-day intervals, from September until mid-December, and also, in Kumasi, weekly in January and February.

The cocoa that was railed in March and April from Ejisu, Bomfa, Konongo and Bekwai had never been sprayed, and a comparison of the Kumasi counts with the average of those of the four other centres might therefore be expected to show whether spraying reduced the build-up of infestation.

At Kumasi, 13,184 bags were sieved, and 4,090 at the other four centres,

TABLE III.

Comparison of infestation in main sheds (sprayed) and verandah sheds (unsprayed), Kumasi, 1958.

Month of sealing	Month of sieving	Type of shed	Average number of insects per bag			
			<i>Lasioderma</i>	<i>Ephestia</i> and <i>Araecerus</i>	Other beetles	Total
February	May	Main	9.2	4.3	18.8	32.3
		Verandah	6.6	6.2	9.0	21.8
January	April	Main	4.3	5.6	18.0	27.9
		Verandah	13.6	3.8	21.2	38.6
January	May	Main	7.4	3.1	20.6	31.1
		Verandah	14.0	5.4	23.8	43.2
January	June	Main	57.5	2.6	65.3	125.4
		Verandah	42.0	7.9	34.9	84.8

Data based on the sieving of 254 bags from the main and verandah sheds of four licensed buying agents.

these numbers being in proportion to the tonnage of cocoa railed. Railing virtually ceased outside Kumasi in April.

The build-up of infestation in Kumasi and in the other four centres was remarkably similar (figs. 1 & 2), so much so as to enhance the validity of making such a comparison, based on counts subject to considerable personal errors.

(6) A more restricted comparison can be extracted from the data. Cocoa of the same seal number was stored in Kumasi in 'verandah' sheds, where it was not sprayed, and in closed sheds, where it was sprayed. The lengths of storage period and the conditions were very similar in these two types of shed. Verandah sheds are considered to be no less conducive to infestation than closed sheds, but the results of counts, summarised in Table III, suggest that there was, on average, no more infestation in the unsprayed verandah sheds than in the sprayed closed sheds. There was thus no evidence from the sieving assessment that spraying reduced the general rate of increase of infestation. The reasons for this will be discussed later.

(7) In the sievings carried out personally or under personal supervision, all the insects seen on the counting tray were collected with a suction-tube and taken to the laboratory. The remaining sievings were also taken back in jars

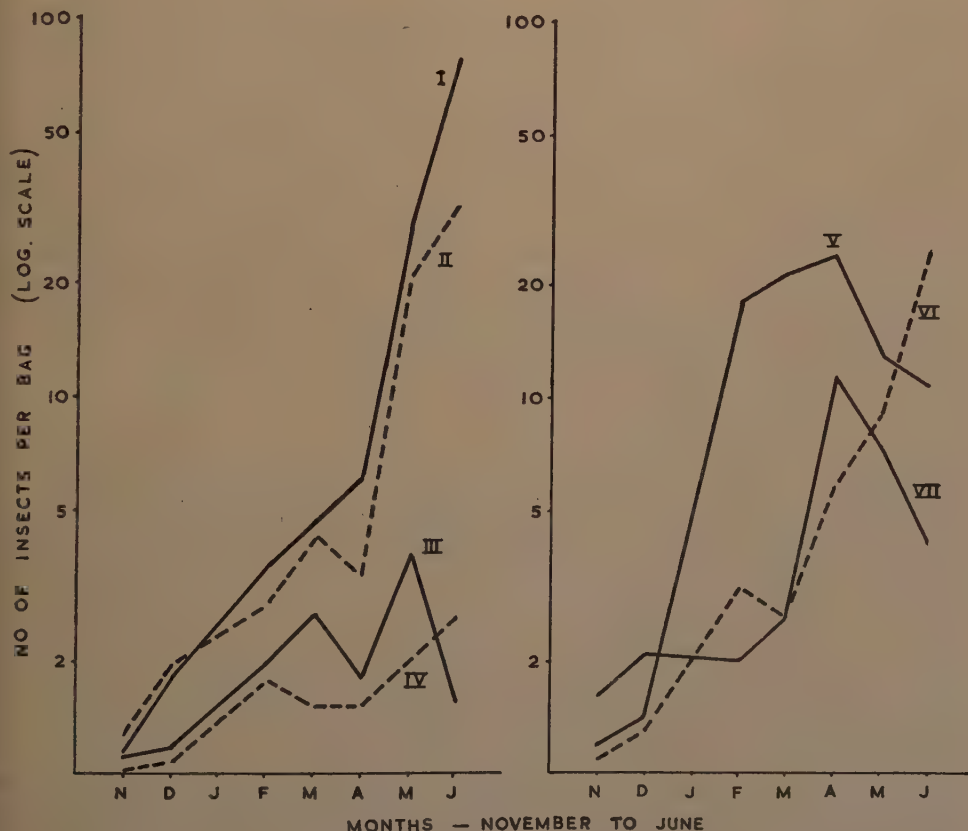


Fig. 3.—The numbers of seven groups of insects in stored cocoa, from November 1957 to June 1958, as determined by sieving. (I) *Lasioderma serricorne*; (II) *Tribolium castaneum*; (III) *Ephestia cautella*; (IV) *Aracercus fasciculatus*; (V) *Cryptolestes* spp.; (VI) *Carpophilus dimidiatus*; (VII) *Ahasverus advena*.

and re-examined for insects that had not been seen on the tray. This method gave information on the liability of missing certain species on the tray, and on the 'apparent' and 'true' relative abundance of the different species occurring. *Cryptolestes* spp. were extremely difficult to see on the tray amongst the broken cocoa and débris. Between December and June, only 12 per cent. of the actual numbers of these species present were found on the tray. For the other species, the number found on the tray, expressed as a percentage of the total number found of the given species, were: *L. serricorne*, 74; *E. cautella*, 89; *A. fasciculatus*, 94; *T. castaneum*, 92; *Ahasverus advena*, 90; *C. dimidiatus*, 73; the *Silvanid* sp., 69; other spp., 57. Thus, all the major species, except *Cryptolestes* spp., can with due care be recognised and counted on the tray, although there is a greater tendency to miss some of the *Lasioderma* and *Carpophilus*.

The increase in actual numbers of the different species, thus assessed, is shown in fig. 3. *Lasioderma* and *Tribolium* were the most abundant in the May and June sievings, and appear to have the greatest capacity for increase on the bulk of stored cocoa. The larvae of these two species were also common in the later sievings, but are not included in the count. *Araecerus* never averaged more than 2.6 per bag; the adults of this species tend to leave the bags, but 'grading' assessment confirmed that the numbers were very low on commercially dry cocoa (that is, with less than 8 per cent. moisture). The numbers of *Ephestia* declined after February–March, when the adult moths were active in greatest numbers in the sheds. The numbers of *Ephestia* developing, considered as a source of infestation of finished confectionery, are quite sufficient to merit the concern of the cocoa and chocolate manufacturers in importing countries. Considered as numbers per bag, however, they are small, and this species does not appear to have the capacity for increase on cocoa shown by *Lasioderma* and *Tribolium*.

Ahasverus advena was the commonest species initially; the occurrence is very irregular and suggests a great sensitivity to moisture content. Of the mould-feeding beetles, *C. dimidiatus* appears to have a greater capacity for steady increase, and was by far the most numerous species on the few bags of the previous main-crop (Subgrade) that were examined.

(8) The evidence shows that Produce Inspection counts were underestimates, the actual numbers present being roughly double the recorded average values. However, this underestimation was, in Ashanti, fairly uniform and does not invalidate the comparisons drawn.

Sources of error in estimates of infestation based on sieving.

The practical purpose of sieving in Ashanti was to select infested cocoa for fumigation, by sampling four bags from a vanload of 320–400 bags. This average is liable in each case to two errors, first, the sampling error arising from the bag-to-bag variation in the numbers of insects present, second, the personal errors of the man sieving and counting.

Sampling errors.—The bag-to-bag variation in degree of infestation is considerable, the size of the variance being roughly proportional to the mean. Sample averages based on four bags or so may differ wildly from the true mean. In fact, the variation within a single stack of cocoa of the same seal number was often as great as the variation between all bags of the same seal number in Kumasi at that time.

In order to base averages on more bags, it would be necessary either to take considerably more bags from a vanload or shipment lot, or to take decisions only on the average values for larger lots, such as complete stacks, or even on all cocoa of the same seal number. The first method would create a volume of work out of all proportion to the gravity of the problem (one per cent. of the crop is roughly 40,000 bags). The second method appears feasible, because it is known that

the development of infestation in a given 'seal' of cocoa is general and fairly uniform throughout all stacks of that seal number. It is apparent when the general average rises above that arbitrarily fixed for fumigation. Reliable averages for this purpose could be based on less than 1 per cent. of the total, and hence would involve less work. From April-May onwards in the 1956-57 and 1957-58 main-crop seasons, the vast majority of bags of all seals in Ghana contained more than 20 insects per bag on sieving, and thus, on the level arbitrarily fixed, the entire end part of the crop merited fumigation.

Personal errors.—Personal errors in insect assessment arise from (i) bad sieving, including insufficient movement of the cocoa on the sieve; (ii) insects' flying away or being blown away, to avoid which sieving should be carried out in a good light but in the shade and out of the wind (*Araecerus* flies very readily but is large enough to be seen); (iii) bad counting, due to lack of attention or to poor light, such as obtains inside sheds (all species except those of *Cryptolestes* can be counted in good light); (iv) incorrect recording. Despite these factors, assessment can be reasonably accurate, given due care and attention. Adequate supervision of staff is essential. In the ports, unlike Ashanti, underestimation due to personal errors was very great, and for this reason is not dealt with here.

Grading.

In the process of the grading of cocoa carried out by the Produce Inspection Department, the different types of defective beans are classified and recorded. 'Defective' includes mouldy, weevilly, germinated, flat or decayed, and 'slaty' beans. Of these defects, those termed 'mould' and 'weevil', the latter covering all kinds of insect damage, are the only types that may, and generally do, increase in storage; 'slate', a defect due to underfermentation, may actually decrease in storage.

Grade I permits not more than 5 per cent. 'slaty' beans and 5 per cent. other defects. In practice, since germinated, flat and decayed beans together amount, on average, to about 2-3 per cent. in Grade-I cocoa, this permits only 2-3 per cent. for 'mould' and 'weevil'. Grade II permits not more than 15 per cent. 'slaty' beans and not more than 10 per cent. of other defects, of which neither 'mould' nor 'weevil' must exceed 5 per cent. Grade III and Subgrade cocoa have no limit on 'slaty' beans; the former permits not more than 15 per cent. of other defects.

It might be expected, therefore, that grading data would yield a vast amount of information on the incidence of 'weevilly' beans, but this is not the case. Beans attacked by insects are usually mouldy also and, since 'mould' has precedence over 'weevil' as a defect, mixed damage is classified as 'mouldy', thus concealing the true proportion damaged by insects. It is only when 'weevil' damage is excessive that it is recorded separately, as when cocoa is downgraded because of insect damage. Hence, the records show only occasional occurrence of 'weevil' damage, at levels very rarely exceeding 1 per cent.

Incidence of insect damage as estimated by grading.

In order to obtain data on the average incidence of 'weevil' damage and its expected increase through the season, arrangements were made with the Chief Produce Inspector to cut and examine fortnightly in 1957-58 a sample of cocoa drawn from a large number of stacks at random. The cocoa that is used for assessing the average weight of beans (the so-called 'bean count') was used for this purpose, this being drawn, in the ports, from all the cocoa arriving and, later in the season, being shipped, and, in Kumasi, from all the cocoa being railed. In each port, 3,000 beans were cut fortnightly, and in Kumasi, 1,500 beans. The data (Table IV) show the progressive increase in percentage defects.

There appears to have been a higher incidence of insect defects early in the season at Accra and Winneba than at Takoradi. The Produce Inspection sieving counts, despite their inaccuracy, show a more rapid build-up of insects at Accra and Winneba, particularly the latter. It is also relevant to point out that Accra and Winneba, particularly the latter, ship a higher proportion of Grade-II cocoa than does Takoradi.

TABLE IV.

Percentage incidence of insect-damaged cocoa beans in assessments at fortnightly intervals, 1957-58.

Period of collection of sample	Sampling centre			
	Takoradi	Winneba	Accra	Kumasi
1957 23.x-7.xi ..	0.00	0.20	0.23	—
8-21.xi ..	0.20	0.27	0.20	—
22.xi-5.xii ..	0.13	0.37	0.10	—
6-19.xii ..	0.07	0.40	0.37	—
20.xii-2.i ..	0.10	0.43	0.57	—
1958 3-16.i ..	0.17	0.43	0.50	—
17-30.i ..	0.27	0.43	0.53	—
31.i-13.ii ..	0.27	0.60	0.53	—
14-27.ii ..	0.67	0.63	0.53	—
28.ii-13.iii ..	0.67	0.67	1.10	0.80
14-27.iii ..	0.83	0.80	0.73	1.00
28.iii-10.iv ..	0.83	0.93	1.17	0.87
11-24.iv ..	0.93	0.97	0.73	1.40
25.iv-8.v ..	1.00	0.97	—	1.07
9-22.v ..	1.06	—	—	1.47
23.v-5.vi ..	1.10	1.00	1.73	—
6-19.vi ..	1.07	—	1.13	1.87

Incidence of live insects.

Arrangements were not made to examine beans at Kumasi until March 1958, when it was started with the additional object of obtaining data on the incidence of living insects inside the beans. It was found, however, that the incidence was too low to be estimated at all accurately unless a very large number of beans was cut. Additional arrangements were therefore made for the collection of all 'weevilly' beans found by Produce Inspection staff in every grading, and the recording of the number cut and defects found. These beans were put immediately into small jars and examined within 24 hours for living insects.

When examining beans, the grader usually cuts and flicks away half of each bean, placing the other half on the table. The number of insects recorded as found, therefore, relates to so many half-beans, and it seems fair to double the percentage incidence to relate it to whole beans. Probably this is an underestimate, because in some beans there may be young larvae, which have not yet rendered the bean visibly defective. In practice, however, it was found that staff were very good at spotting even a tiny amount of insect frass.

Of 21,000 beans cut and examined at Kumasi in April and (mostly) May 1958, 292 (1.38 per cent.) were found to be 'weevilly'. Of these, 118 were examined and classified into damage by moth or by beetle; 30 contained moth frass and the remainder beetle frass, suggesting that at this period about one-quarter of the

defects were due to moth. Associated with the 292 defective beans the following living insects were found:

As larvae.—*Lasioderma*, 18; *Ephestia*, 4; *Araecerus*, 5; *Tribolium*, 4; *Cryptolestes*, 6; other larvae (including those of *Ahasverus* and *Carpophilus*, which are difficult to distinguish), 14; total larvae, 51.

As adults.—*Lasioderma*, 1; *Cryptolestes*, 9; *Carpophilus*, 2; undetermined species of *Silvanid*, 1; total adults, 13.

The number of larvae found per bean was usually one, sometimes two, and on one occasion, three. Taking the above numbers as one insect per bean, which was the general case, and doubling them because only half of each bean could be examined, they represent a percentage incidence in beans of 0.61 living insects, including 0.49 larvae, and 0.17 larvae of *Lasioderma*. *Lasioderma* was clearly causing most damage to the beans; *Araecerus* was much less common.

There was a progressive accumulation of defects caused by attacks of insects, particularly *Lasioderma* and *Ephestia*, although, late in the season, live insects are found in only a proportion of defective beans. The very small percentage incidence in beans nevertheless means a considerable number of insects per bag; as there are over 60,000 beans per bag, an incidence of 0.5 per cent. implies over 300 insects per bag.

The very small percentage incidence of insects demands that a great many beans be examined to obtain accurate data. Taking the present data (which represent only one point in the seasonal increase) as an example, an infestation by living insects of approximately 0.6 per cent. of the beans was related to accumulated defects of 1.0–1.5 per cent. at a time when personal assessment of sieving results showed about 40–80 insects 'free' in the bag. A detailed study might be rewarding and might establish a correlation between the insect population estimated by sieving and the cumulative total of insect defects.

Upper limit of insect incidence.

There appears to be a limit to the possible incidence of insect attack on cocoa, at any rate on commercially dry cocoa. Only very rarely indeed, at the end of the 1956–57 main-crop season were bags detected with over 5 per cent. insect defects. In all, seven such bags were found, having up to 13 per cent. insect-damaged beans; this involved only 18 tons of cocoa. Such records are very rare. The average incidence of insect defects in the whole of the 1957–58 main crop was certainly under one per cent. The highest figures occur late in the shipping season in Takoradi, which, of all the ports, stores cocoa for the longest period.

Estimate of quantitative losses from insect attack.

An attempt was made, with the very small number of defective beans available, to estimate roughly the weight loss in cocoa from insect attack. In three lots of 50 defective half-beans, the frass and insect material was cleared out as well as possible and weighed and the remaining half-beans weighed. The remaining half-beans weighed 25.3, 24.8 and 23.9 g., respectively. The insect material and frass (weighed without drying) weighed 1.2, 1.4 and 0.9 g. Fifty sound half-beans from the same lots weighed 26.1 g.

On this evidence, the actual loss in weight of cocoa due to an insect attack causing, say, one per cent. of the beans to be defective (and 1% insect defects would be an unusually high value for the whole crop), must be less than 0.05 per cent.; alternatively, regarding it in terms of contamination of cocoa, such a level of insect infestation would result in there being under 500 parts per million of insect matter in the cocoa. As the calculation is based on the weight of the insect matter before drying, presumably this figure would be reduced considerably when the beans are broken into nib and roasted in manufacture.

ORIGINS AND DEVELOPMENT OF INFESTATION.

The general picture of infestation in cocoa, as judged from the 1956-57 and 1957-58 main-crop seasons, is of a very light but fairly general infestation occurring early in the season, becoming a problem through the development of *Ephestia* after 2-3 months' storage, and causing significant damage, chiefly on account of the development of *Lasioderma*, after 4-5 months' storage.

All the insects occurring in cocoa are capable of breeding on a variety of other foodstuffs present in Ghana, and usually more rapidly than on cocoa. Cocoa is, in fact, one of the least satisfactory foods for most of them, including *Lasioderma* (Howe, 1957) and *Tribolium*, which nevertheless become the most abundant species. A great variety of stored-products beetles enter cocoa before it comes into licensed sheds, but only eight species breed in it to any extent.

It is difficult to see how any effective measures can be taken to prevent the very light initial infestation of cocoa, or to reduce it significantly. No single source was found that appeared to contribute markedly to infestation. The picture was instead one of many sources, all of which contributed a little.

Farmers' and brokers' stores were examined in many villages, together with the drying trays used for cocoa after fermentation, and other village features, such as corn and rice mills, and local food markets. The stores were generally clean, and infestation, though involving most of the species found in cocoa, was very light. The hygiene in licensed buying agents' stores is, with very few exceptions, of a high standard and infestation of the structure of the sheds is very light or non-existent. Certainly this is the case in up-country stores, many of which stand clean and empty for several months between seasons.

Prior to the opening of the 1957-58 main-crop season, not a single live insect was found in the fabric of sheds sprayed with pyrethrins the previous season, and only a very few (including *Ephestia*) in sheds not previously sprayed. It seems very unlikely that endemic infestation in these sheds has at any time in the past few years resulted in significant cross-infestation of cocoa coming into store.

Cross-infestation from produce other than cocoa, stored outside the licensed sheds or occasionally inside them, is certainly not serious in Ghana. There is, of course, no other major crop, and there is very little storage of other produce in or near cocoa sheds. Small quantities of maize, maize meal, palm kernels, pulses and coffee were examined and were never more than lightly infested. In Takoradi port, a limited amount of other produce, such as palm kernels or copra, is stored more commonly in the port sheds, and here cross-infestation can be a problem.

Until the end of December in up-country stores, very few insects were seen, either flying or resting on the walls, or knocked down by spray. Thus the impression was gained that infestation from outside sources could at most be very light.

The cross-infestation of the new crop by the infested remnants of the previous crop is strictly limited, but may occur in two ways. First, in Takoradi, shipment is so prolonged that substantial quantities of the old crop may remain in store at the commencement of the new crop. Thus 1,500 tons of 1956-57 cocoa, including Grade-III and Subgrade cocoa, remained in Takoradi port sheds at the commencement of the 1957-58 season. Secondly, old and probably infested cocoa may be illegally mixed with new cocoa, to add weight but not in sufficient quantities to lower the grade. A few cases of this practice detected by the Produce Inspection Department were studied and were found to have increased substantially the infestation of small lots of cocoa. However, such cases were rare in Ashanti in the 1957-58 season.

Another form of mixing involves the storage of good-quality November or December cocoa, unsealed, for bringing up the quality of late-season cocoa brought

in for grading in February or March. Generally, the December cocoa, although of good quality, has the higher infestation because of its longer storage. The blend must then await movement in order of seal number, with the result that the original December cocoa is stored longer than it otherwise would be. Only one example of this practice was noted in the 1957-58 season, and the resulting cocoa was, by May, the most heavily infested in Kumasi.

Lastly, we may consider the natural movement of infestation within the crop itself in storage. Since infestation in the 1957-58 main crop in Ashanti was light but generally distributed, there were in fact no localised foci of infestation from which it spread. Differences developed between 'seals' due to length of storage, but it does not seem likely that cross-infestation from stack to stack is of more than slight importance in the development of infestation. Spraying measures certainly reduced very greatly the number of live insects to be seen in the sheds and on the outside of stacks. They did not appear, however, to affect appreciably the general rate of increase of infestation.

It is of particular importance to know whether *Ephestia* adults must emerge from the stack in order to mate. Stacks are usually built so that there is an interconnecting 'lattice' of sizable spaces between the bags. *Ephestia* adults occurred in the inter-bag spaces right through the stacks and it seems likely that they are able to mate and oviposit there without coming out of the stack. This behaviour is notably different from that observed in English warehouses in the case of the development of *Ephestia elutella* (Hb.), of which the mature larvae migrate chiefly to the outside surface of the stack to pupate. In Ghana, pupation of *E. cautella* takes place on bags throughout the stack more or less evenly.

CLIMATIC CONDITIONS IN COCOA SHEDS.

Cocoa sheds in Ghana are constructed in various ways, which affect to a limited extent the internal temperatures and humidities. An attempt was made to assess the magnitude of these differences in relation to the possible effect on development of infestation. Data are given from sheds in Kumasi and Ejisu, which are typical of large up-country sheds used for the longer-term storage of cocoa. Conditions in port sheds are known to be not markedly different.

About half the sheds in Ghana are constructed of corrugated iron (or steel) sheets, painted black or dark red, for the walls and roof, with 'eaves ventilation' of twelve inches or so under the overhang of the sloping roof. Most other sheds have 'swish' walls made of laterite mud blocks, with the surface cement-rendered inside and out, and with concrete pillars for support. Occasionally, the walls are entirely of concrete blocks. The roofs are of painted corrugated iron, unpainted aluminium, or asbestos, and in all but a few cases there is a ventilation space at the eaves. A very few sheds have no eaves ventilation, but small windows or louvres. Doors are normally large, and are open most of the day in the working season.

The main constructional point affecting internal temperatures is the structure of the roof. Sheds with roofs of unpainted aluminium, which tends to reflect radiant heat, have slightly lower day-time temperatures at their lower levels, and considerably lower temperatures near their roofs, than sheds with painted iron roofs. Asbestos roofs have an intermediate effect. The construction of the walls has less effect, though sheds with corrugated-iron walls are hotter at their lower levels than sheds with concrete or swish walls. The absence of eaves ventilation does not make sheds excessively hot.

The maximum temperatures recorded in 1957-58 in four sheds of differing construction at Kumasi from December to April, and two sheds at Ejisu in December and January are given in Table V. The temperatures were recorded six feet above the floor and away from the walls. The minimum (early morning)

TABLE V.

Temperatures (°F.) recorded in six Ashanti storage sheds.

Shed no.	Constructional details	Range of monthly mean maxima	Range of daily maxima	Average daily range
1	Sheet-iron roof and walls, painted red; eaves ventilation	94-99	88-105	19
2	Sheet-iron roof, painted black; concrete walls; no eaves ventilation	93-97½	85-102	16
3	Asbestos roof; concrete walls; limited eaves ventilation ..	90-95	84-99	16
4	Unpainted aluminium roof; sheet-iron walls; eaves ventilation ..	86-91	82-95	13
5	Sheet-iron roof and walls, painted black; eaves ventilation ..	94, 94	88-100	19
6	Unpainted aluminium roof; walls of concrete and 'swish', cement-rendered; eaves ventilation ..	87, 87	84-89	12

Temperatures recorded at a level of six feet above the floor.

TABLE VI.

Atmospheric temperature and humidity in cocoa sheds.

Shed no.	Position	Temperature (°F.) and relative humidity (%)					
		9.0 a.m.		12 noon		3.0 p.m.	
		°F.	%	°F.	%	°F.	%
1	Top of stack	87	67	100	48	104	42
	Six feet above floor ..	80	73	84	78	90	47
	External shade ..	80	79	83	79	90	46
7	Top of stack	86	68	88	60	100	40
	Six feet above floor ..	80	79	82	75	90	51
	External shade ..	79	83	82	78	90	50
8	Top of stack	80	79	85	69	92	45
	Six feet above floor ..	79	82	81	77	83	59
	External shade ..	79	85	82	67	89	44

Means of values recorded on 12 days in February 1958.

The construction of shed no. 1 is given in Table V; shed no. 7 and shed no. 8 are like nos. 5 and 6, respectively, in that table.

temperature in each of these sheds was within 2–3°F. of the same figure each day, and averaged 75°F.

The comparison between conditions on the top of stacks, usually at the level of the eaves, and at lower levels, is illustrated by the data in Table VI. These are from recordings made in February, one of the hottest months. Conditions at the lower levels in corrugated-iron sheds, were almost identical with external shade temperatures and humidities, provided the doors were wide open (as is usual in the working season in the day-time). In sheds like no. 6 and no. 8, with unpainted aluminium roofs, conditions were a few degrees cooler, and less dry, in the afternoons. On top of cocoa stacks, a few feet under the roof, temperatures in iron-roofed sheds were 10–14°F. higher than the outside air temperature.

These differences affect the actual temperature of the cocoa only slightly. The temperature of the cocoa was measured by spear thermometers, six inches long, inserted to reach the centre of a bag from the flat side. Measurements were also made of the moisture content using a calibrated Scot-Mec Oxley moisture meter with a tropical scale, and conversion chart for cocoa. The data obtained in February in the three sheds of Table VI are illustrated in Table VII.

TABLE VII.

Temperature and moisture content within bags of cocoa in three sheds in Kumasi, February 1958 (means, followed by range).

		Shed no.		
		1	7	8
Moisture content (%)	Top layer	6 (5½–6½)	6 (5½–6½)	7 (6½–7½)
	Upper half of stack ..	7½ (6½–8½)	6 (5½–6½)	8½ (no range)
	Lower half of stack ..	7½ (6½–8½)	8 (7½–8½)	8½ (7½–9½)
Temperature (°F.)	Top layer	88 (85–90)	87 (84–90)	84 (82–88)
	Upper half of stack ..	84 (82–87)	85 (81–87)	82 (80–84)
	Lower half of stack ..	82 (82–86)	84 (80–86)	81 (80–84)

Shed no. 1 was the hottest shed in Kumasi and shed no. 8 the coolest; the difference between the temperature of the cocoa in them is very slight, even in the top layer, which on its upper surface is subject to day-time temperatures over 100°F. in the hotter sheds.

Cocoa picks up and loses heat slowly, so that the internal temperature of cocoa in bags is never far from the daily mean temperature inside the shed, that is, 82–84°F. Measurements have been made in most sheds in Kumasi, and also in the ports, and recordings made well inside the bags were always in the range 80–92°F. No average over a period was outside the range 82–88°F. This applies also to verandah sheds and external stacks under tarpaulins. Cocoa bags remaining in the sun have reached 120°F. on the hessian sack, and 114°F. one inch under the hessian, but 4–5 in. from the surface of the sack, within the cocoa, the temperature was 92°F.

There was a lower moisture content in the top layer of bags than in the rest of the stack, but otherwise little gradation from top to bottom, except for the 2–3 layers nearest the floor, which generally had a higher moisture content than the rest. This is probably due to upward movement of water-vapour through the concrete floors.

It is clear that such temperature differences as exist between sheds of differing construction have a very limited effect on the internal temperature of the bags

of cocoa, and temperatures in the cocoa never exceed the critical for any species of insect involved. As far as this investigation went, cocoa was about one per cent. less in moisture content in iron sheds than in sheds with unpainted aluminium roofs. This difference, though small, may be of practical importance if cocoa ever exceeds 8 per cent. moisture content. Dade (1929) showed that the growth of moulds increases considerably at moisture contents over 8-9 per cent. 'Mould' is a defect of stored cocoa beans having precedence over insect attack, and roughly three times as common. There was evidence, which requires to be substantiated, that a higher percentage of 'mould' defects occurred in the cooler sheds. No differences in insect infestation were attributable to the type of shed construction.

It is not to be expected that the speed of insect development will vary appreciably within the very small range of temperatures in cocoa. Low moisture contents, on the other hand, are advantageous in restricting the development of moulds, mould-feeding beetles and *Araecerus*. The construction of sheds should, therefore, aim at producing the hottest and driest conditions attainable. The popular construction of corrugated iron or steel, painted black or dark red, is very suitable; moreover, the fabric of this type of shed becomes too hot in the day-time to support endemic infestation. Roofs of unpainted aluminium sheeting, which have become more popular in recent years, have a marked effect in rendering a shed cooler and less dry, whether the walls are 'swish', concrete, iron or steel.

There seems no point in the customary 'uncontrollable' ventilation space at the eaves, provided other controllable ventilation by doors and windows is adequate. Such ventilation can be closed when external conditions are humid, and opened in dry sunny weather. The absence of eaves ventilation would not render working conditions in the shed too hot.

CONTROL MEASURES.

The present work makes possible a revaluation of the infestation problem in stored cocoa. Secondly, it is relevant to consider the purpose of spraying in relation to cross-infestation of cocoa. Thirdly, some factors affecting the use of pyrethrum-in-oil films on stacks of bagged produce under tropical conditions may be considered.

Considering the first point, *Lasioderma serricorne* is clearly the species causing the greatest actual damage to cocoa beans, and is probably the only species present that is worthy of concern on this score, but the damage is very small in terms of weight loss, certainly less than 0.1 per cent. of the whole crop. Potentially, it can have a substantial effect on quality, although for the past few years in Ghana only very small amounts of cocoa have been downgraded to Grade III or Subgrade by reason of a high incidence of insect defects. A substantial quantity is downgraded from I to II, and insect defects are an important contributing factor, but Grades I and II have for some years fetched the same price. If a price differential operated, *Lasioderma* would be economically more important.

Lasioderma reached significant numbers, associated with 1 per cent. or more insect-defective beans, only after five to six months' storage. This observation is very similar to that of Riley (1957) in Nigeria, who likewise observed that *Ephestia* adults became numerous in the sheds in February after two months' storage. He showed that the percentage of beans containing larvae of *Ephestia* was at all times very small and did not increase as did the percentage that included *Lasioderma*. The present data confirm the relatively small numbers of *Ephestia cautella* per bag. Nevertheless, this species is present in sufficient numbers to concern the cocoa and chocolate manufacturers as a source of infestation in finished confectionery. A large proportion of the crop is seriously infested with *Ephestia* in this respect, a very much larger tonnage than is seriously

damaged by *Lasioderma*. *Ephestia* infestation must therefore be considered the major reason for control measures.

On the second point, the purpose of control measures was to reduce the build-up of infestation in cocoa by preventing cross-infestation from outside sources, from more heavily infested cocoa, and from endemic infestation in the sheds. In the United Kingdom, pyrethrum spraying has proved effective in controlling endemic *E. elutella* in warehouses. It was, therefore, logical to hope that it would considerably reduce *E. cautella* in Ghana, were spraying effectively carried out at more frequent intervals, to compensate for the shorter toxic life of pyrethrum under tropical conditions.

Although the comparison of infestation in sprayed and unsprayed sheds cannot be considered precise, there can be no doubt that spraying measures did not substantially reduce the development of *Lasioderma* or other beetles, nor was *Ephestia* controlled to a degree comparable with experience in the United Kingdom. Observations suggest that cross-infestation was of little importance in the build-up of infestation, which developed to a large extent internally in stacks of bagged cocoa from very light but widely distributed primary infestations that existed in the cocoa when it came into store. Film spraying of the surfaces of stacks does not affect appreciably the development of insects inside the stack, although it might be expected to have a marked effect on *Ephestia*, the adults of which emerge from the stack more than those of *Lasioderma* and other beetle species. However, the behaviour of *E. cautella* in Ghana passing through its developmental life in all internal parts of the stack is probably of great importance in this respect.

Since cross-infestation is believed to have had little effect upon the build-up of infestation, the comparison between sprayed sheds and unsprayed sheds does not measure the potential value, under tropical conditions, of films of synergised pyrethrum-in-oil in protecting bagged produce from cross-infestation. Mention may be made of certain conditions occurring in Ghana which are very different from those pertaining in Britain. In applying the spray, a considerable proportion is lost through the eaves ventilation present in most sheds. Apart from the waste of insecticide, the fact that sheds will not hold an insecticidal fog makes the attainment of an even film much more difficult. The films attained in practice tended to be unevenly distributed but were probably heavier on average than those recorded in Britain (Pest Infestation Laboratory, Slough—Private communication). The dosage used was greater.

In Ghana, cocoa bags are stacked on wooden dunnage, which allows easy movement of insects under the stack, where they do in fact tend to collect in spilt beans and debris, but it is impossible to spray this under-surface. Also, the top surfaces of storage stacks are generally level with the eaves of the shed and these surfaces are generally subject to temperatures of 100–110°F. in the day-time, together with lower air humidities than external conditions. White-oil deposits dry up fairly rapidly under these conditions; more quickly than on the sides of stacks. The loss in weight of oil was estimated on 'target' squares of hessian, sprayed under normal conditions. The moisture uptake and loss had to be estimated and allowance made for it. Fig. 4 shows the results obtained on the horizontal top surface and lower side surfaces in two sheds.

The insecticidal 'life' of pyrethrum-in-oil films under climatic conditions in cocoa sheds in Ghana requires investigation. Apart from the high temperatures and humidities prevailing, the light intensity must be generally higher than in warehouses in the United Kingdom, particularly near the doors. This aspect could not be fully investigated, but a few experiments were carried out in which different species of insects were confined on films obtained in practice, under store conditions. Results were very variable, and the build-up of oil, from frequently repeated spraying, is a complicating factor. Tentatively it may be stated that

the toxic life of pyrethrum in heavy films (1500 mg. per sq. ft. or more) appeared to be of the order of two or three days for the more susceptible species, including *Ephestia cautella* adults, *Ahasverus advena*, *Cryptolestes* spp. and *Carpophilus dimidiatus*. In the darkest and coolest parts of sheds, some effect was noted for up to seven days. *Tribolium castaneum* and mature *Ephestia cautella* larvae were very resistant, even to direct spraying. Oil alone, however, is toxic to some

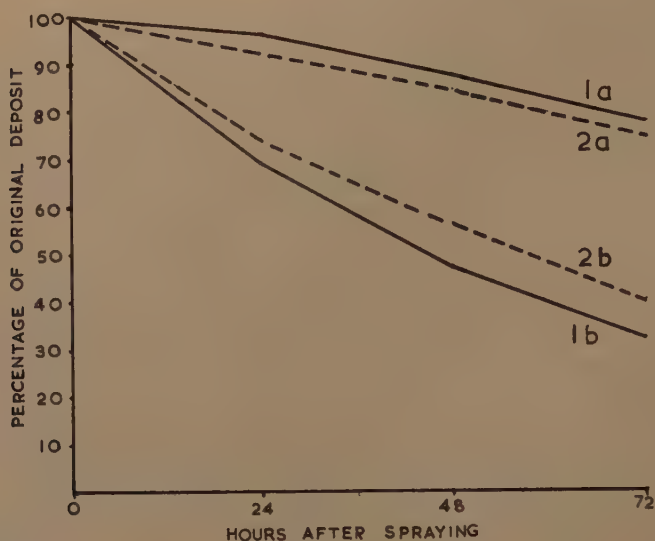


Fig. 4.—The loss in weight from a film of synergised pyrethrum in white oil sprayed on hessian sacks, (a) on the lower vertical side of the stack, (b) on the top of the stack, in each of two sheds, (1) and (2). Each graph represents the average of two experiments.

species, particularly *E. cautella* adults and *A. advena*, and the oil deposit may persist for much longer than three days. In any event, the 'life' of films is relatively short and it may be that in many instances in the tropics, pyrethrum in technical white oil can be used more effectively when applied frequently as a light mist for controlling adult flying insects.

Summary.

In Ghana, a considerable part of the main-crop cocoa is stored for six months or more, some up to nine months, and infestation by insects increases during storage. Data are given, obtained chiefly in Ashanti on the 1957-58 main crop.

Assessment by sieving the contents of whole bags and counting the numbers of adult insects found (or, in the case of *Ephestia cautella* (Wlk.), the larvae and pupae also) showed that at the beginning of the main-crop season (September-November), infestation was very light (1-2 insects per bag), but was present in a high proportion of the bags (46-47 per cent. in October). The species present represent those found regularly breeding in cocoa in Ghana, namely, *Ephestia cautella* (Wlk.), *Lasioderma serricorne* (F.), *Araecerus fasciculatus* (Deg.), *Tribolium castaneum* (Hbst.), *Carpophilus dimidiatus* (F.), *Ahasverus advena* (Waltl), *Cryptolestes* spp., and an unidentified species of Silvanid. After six months'

storage, the total count averaged over 100 per bag and comprised chiefly *L. serricorne* and *T. castaneum*; larvae of *Ephestia* were much rarer (less than five per bag), but adults of *Ephestia* were abundant in the sheds after 2-3 months' storage.

Sieving proved a useful technique for obtaining data on infestation, though careful supervision of staff is required to minimise errors. Variation from bag to bag in the same 'lot' of cocoa is large, and estimates based on as few as four bags are unreliable.

Assessment of insect damage on samples of cocoa beans taken fortnightly by spear-sampling showed an increase from 0.20 per cent. insect-defective beans in November to 1.0-1.9 per cent. in June. Of 21,000 beans examined in April and May, *L. serricorne* occurred in 0.17 per cent., and 0.6 per cent. contained living insects. Damage by insects affecting more than 2 per cent. of the beans has been very uncommon in Ghana in the past few years. The effect on quality, as assessed by commercial grading and considered financially, is at present slight, as it also is in terms of loss of weight over the whole crop (certainly less than 0.1 per cent.). *E. cautella* is the most important species economically, because it can infest the premises of cocoa and chocolate manufacturers in importing countries, and spread to finished confectionery. It affects a large portion of the crop in significant numbers.

The primary infestation of cocoa before it comes into licensed storage occurs in thousands of small farms and villages, and no one district or type of source is of special importance. Increase of the infestation during storage occurs chiefly as a development of this primary infestation; cross-infestation from outside sources is relatively unimportant.

The application of synergised pyrethrin in white oil within storage sheds as a fog, from which a film was deposited on the stacked bags of cocoa, was carried out in many sheds at intervals of 3-4 days, and a comparison made between sprayed and unsprayed sheds, based on data from sieving. Spraying did not substantially reduce the development of infestations of *L. serricorne* or other beetles, nor was *E. cautella* controlled to a degree comparable with experience of similar treatment against *E. elutella* (Hb.) in Britain; this may be due to the fact that *E. cautella* in Ghana develops in bags throughout the stack, and not chiefly in the peripheral bags, as does *E. elutella* in Britain.

Conditions affecting the film-spraying of bagged cocoa in Ghana differ greatly from those in Britain. Uncontrolled ventilation at the eaves of sheds results in a considerable loss of insecticidal fog, and uneven distribution of deposit; the under-surface of the stacks cannot be sprayed, because they rest on wooden dunnage; it is difficult to maintain an effective oil-film on the topmost horizontal surfaces of the stack, near the roof, of which the temperature frequently exceeds 100°F.; deposits probably do not retain their toxicity for more than a few days.

Variations in the materials from which cocoa-storage sheds are constructed, and in their design, cause relatively small differences in internal climatic conditions, and these have even less effect on the temperature of the cocoa in bags, which is generally in the range 82-88°F. The moisture content of the cocoa was about one per cent. less in a hotter type of shed than it was in one of a cooler type, and it is considered that the construction of sheds should aim at producing the hotter, drier conditions that are attainable, in order to keep moisture contents down and restrict the development of moulds, mould-feeding beetles and *Araecerus fasciculatus*.

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References.

- 112145 COTTERELL, G. S. (1934). Infestation of stored cocoa by weevil (*Araccerus fasciculatus*) and moth (*Ephestia cautella*).—*Bull. Dep. Agric. Gold Cst* no. 28, 14 pp.
- 0 201 COTTERELL, G. S. (1952). The insects associated with export produce in southern Nigeria.—*Bull. ent. Res.* **43** pp. 145–152.
- DADE, H. A. (1929). Internal moulding of prepared cacao.—*Bull. Dep. Agric. Gold Cst* no. 16 (*Yearb. 1928*) pp. 74–100.
- DEPARTMENT OF SCIENTIFIC AND INDUSTRIAL RESEARCH (1958). Pest infestation research 1957.—55 pp. London, H.M.S.O.
- HOWE, R. W. (1957). A laboratory study of the cigarette beetle, *Lasioderma serricorne* (F.) (Col., Anobiidae) with a critical review of the literature on its biology.—*Bull. ent. Res.* **48** pp. 9–56.
- 45 217 RILEY, J. (1957). A survey of the build-up of infestation in bagged cocoa beans in store in Western Nigeria.—*Bull. ent. Res.* **48** pp. 75–78.

BIOLOGICAL CONTROL OF THE COCONUT SCALE, *ASPIDIOTUS*
DESTRUCTOR SIGN., IN PRINCIPE, PORTUGUESE
 WEST AFRICA.

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In 1952, on the coast near the village of San Antonio in the island of Principe in the Gulf of Guinea, yellowing leaves were noticed on a small area of coconut palms. It was thought that this was merely the result of dry weather. However, this yellowing did not recover during the rainy season but gradually spread, and in November 1954 it was found to be due to the coconut scale, *Aspidiotus destructor* Sign., which had not been previously recorded in Principe, nor in the neighbouring island of S. Tomé. This scale is a pest of coconuts throughout most of the tropics.

Dr. A. Castel-Branco of the Portuguese Junta de Investigações do Ultramar went to Principe in August 1955 having made arrangements with the West Indian Station of the Commonwealth Institute of Biological Control for shipments of the Coccinellid, *Cryptognatha nodiceps* Mshl., to be sent to him in Principe for the biological control of the scale.

Three shipments were made from Trinidad, W.I., in August 1955, of adult Coccinellids collected on coconut palms in association with *A. destructor*. A total of 3,330 Coccinellids was sent, comprising 2,455 examples of *C. nodiceps*, 455 of *Azya trinitatis* Mshl. and 420 miscellaneous, including examples of *Chnoodes* sp. nr. *cinctipennis* Gorh., ? *Cleothera* sp., *Exoplectra dubia* Crotch, *Hyperaspis* sp., *Pentilia insidiosa* Muls. and ? *Prodilis* sp. The species in addition to *Cryptognatha nodiceps* were sent since they were all found in association with *Aspidiotus* on coconuts in Trinidad and it was thought that if *Cryptognatha* proved unsuitable another of these species might prove useful.

Details of these shipments, the state of the scale attack at that time, and the method of handling the material on arrival in Principe are given by Castel-Branco (1956, 1959). As was expected, there was a fairly heavy mortality (67.6%) during the long air journey from Trinidad to Principe, but sufficient material of *Cryptognatha* arrived alive for both liberations and breeding stocks. From the latter a large amount of additional material was bred and liberated. None of the other species became established in Principe.

By the end of 1955 (Castel-Branco, 1956) *Cryptognatha* was well established, was multiplying very rapidly in the field and was destroying *Aspidiotus* most satisfactorily.

In March 1956 a visit was arranged to Principe in order to check on the progress made in the biological control of *Aspidiotus*, with the possibility that additional species of Coccinellids might be tried if the situation warranted it.

Effect of *Aspidiotus* on copra production.

The island of Principe lies about 2° north of the equator and 150 miles west of Rio Muni, West Africa. It is about 20 miles long from north to south, and 10 miles from east to west.

The temperature is very uniform over the island and throughout the year, but there is considerable variation in rainfall; the northern part of the island is

the driest, the southern the wettest. Actual temperature and rainfall data are given (fig. 1) for Esperança estate in the north-central part of the island and it is probable that the seasonal and annual variations seen here are typical of the

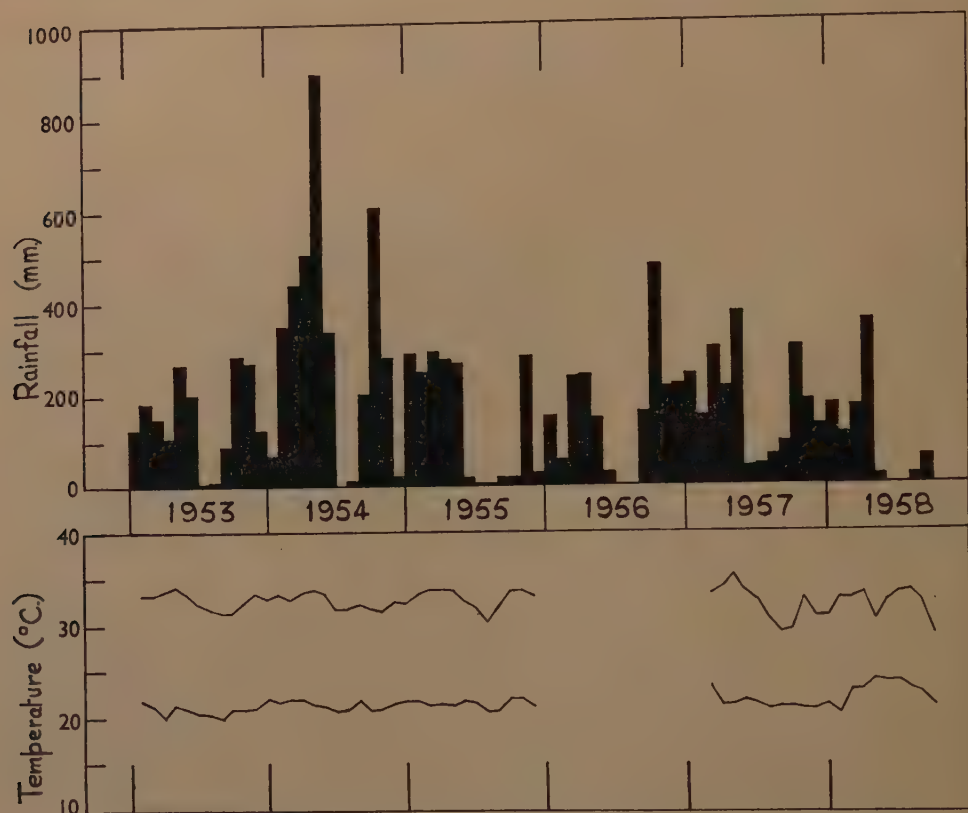


Fig. 1.—Histogram showing rainfall data for Esperança, Principe, and graph of mean monthly maximum and minimum temperatures for the period 1953–1958.

whole island. As is seen from fig. 1, there is a marked dry season starting in June or July (a month earlier in 1958) and lasting until the beginning or middle of September (end of October in 1955). There appears to be a short dry season about December or January but this may not be marked.

Copra production is very dependent on adequate rainfall, high rainfall with a poorly marked dry season is usually followed a year or so later by high production.

TABLE I.

Copra production in Principe (kilos).

1946	—	1,281,652	1953	—	1,322,643
1947	—	1,588,513	1954	—	1,467,964
1948	—	1,341,130	1955	—	997,376
1949	—	1,404,241	1956	—	525,061
1950	—	1,379,696	1957	—	608,000
1951	—	1,226,895	1958	—	730,000 (6 months)
1952	—	1,339,547			

Conversely a year of abnormally low rainfall or a prolonged severe dry season is followed later by a decline in production.

The annual copra production of Principe as a whole since 1946 is given in Table I. Between 1946 and 1954 there was a certain amount of annual fluctuation, but the production was consistently around 1,400 metric tons. However, in 1955, following what was, with regard to rainfall, a very favourable year, there was a considerable drop in production. This was entirely due to the ravages of *Aspidiotus destructor* which was by this time extremely abundant over most of the important coconut-growing areas.

In the succeeding years 1956 and 1957 production was even lower. However, with the successful biological control of the scale, production was back to normal again in 1958.

Copra production is most concentrated in the northern areas of the island and in the south-east. Many coconut palms are grown in the rest of the island, but very often in mixed cultivations. It is of interest to compare the trends of monthly copra production on several estates in different parts of the island to



Fig. 2.—Island of Principe showing positions of the larger estates and their subdivision. (a) Sociedade Agricola do Sundy, (b) Companhia Agricola do Bela Vista, (c) Sociedade de Agricultura Colonial, (d) Companhia do Ilha do Principe. (1) Sundy, (2) S. José, (3) Esperança (Port Real), (4) S. Joaquim, (5) S. Carlos Fundão, (6) A. Andrade, (7) Francisco Mantero, (8) Infante D. Henrique.

obtain, if possible, a more detailed estimate of the reduction of yields due to the spread of *Aspidiotus*, and the effect of the introduction of *Cryptognatha*.

The distribution of the larger copra-producing estates and the position of the divisions from which separate figures of copra production are available are shown in fig. 2. The approximate position of the original point of introduction of *Aspidiotus*, the Bay of San Antonio, is also given.

The monthly copra productions for these estates, which range from Sundy in the north to Infante D. Henrique in the south, are shown in fig. 3, the figures from both the latter and Sundy are the aggregate totals of large estates, the others from comparatively small areas. Infante D. Henrique is also somewhat different from the others in that until 1953 this large property was practically abandoned. Since that time secondary bush growth has been cleared progressively from amongst the palms, and copra production should therefore have increased steadily. The graph for production of oil-palm kernels is also given (fig. 3) as an indication of the extent of the rehabilitation of the estate, and the general trend that would have been expected with copra production.

Figures for copra production show great variation from month to month. With a coconut crop this is almost inevitable since cutting of ripe nuts on the palms and collection of fallen nuts depends to a certain extent on available labour, and if all suitable nuts are gathered from the palms throughout an estate during one month, no collection may be necessary for over a month following this. In order to smooth out these monthly variations, which do not in fact represent variation in actual coconut yields, the original data has been 'averaged.' Figures for two monthly periods have been averaged, and the averages thus obtained have been similarly treated. Thus if J, F, M, and A are the yields in January, February, March and April then the final figures on which the graphs have been based have been obtained as follows:—

J

$$\frac{J+F}{2}$$

F

$$\frac{J+F+F+M}{2 \times 2} = \frac{J}{4} + \frac{F}{2} + \frac{M}{4}$$

$$\frac{F+M}{2}$$

M

$$\frac{F+M+M+A}{2 \times 2} = \frac{F}{4} + \frac{M}{2} + \frac{A}{4}$$

$$\frac{M+A}{2}$$

A

In other words the final figures used represent the recorded monthly figure for that month averaged with half that of the previous month and half that of the succeeding month.

It is seen from fig. 3 that a steady decrease in the copra production of the various centres began *approximately* during the months listed below.

1. Sundy	January 1955
2. S. José	June 1955
3. Esperança	May 1955
4. S. Joaquim	August 1955
5. S. Carlos Fundão	August 1955
6. Anselmo Andrade	August 1955
7. Francisco Mantero	October 1955
8. Infante D. Henrique	November 1955

This is seen more clearly from the original data, which for reasons of economy have not been published in detail, but which may be obtained, if required, from the author.

As stated above, the long dry season of 1955 would have affected yields adversely, but only after some time lag. The decline in production from the separate estates started in January 1955 before this severe dry season and took about ten months to spread from north to south. This decrease on each estate follows the general course of the spread of *Aspidiotus* over the island.

Status of *Aspidiotus destructor*.

From its initial point of introduction in the Bay of San Antonio the scale first became a serious pest in the drier northern parts of the island, and then spread comparatively slowly southwards. It was noticed on the south-west coast in September 1954, but was not considered as a serious pest in that part of the island until some two years later.

It might be noted here that a suggestion has been made (Dr. A. S. Balachowsky, private communication) that the form of *A. destructor* present in Principe is that generally found in Asia and East Africa, rather than that found in West Africa, and that the Asian form is a more serious pest than the latter. Dr. D. J. Williams of the Commonwealth Institute of Entomology, however, states that both forms are found in any population of *A. destructor* and that the existence of two distinct races is unlikely. This point is of interest in connection with the actual area of origin of the material accidentally introduced into Principe. It would seem more likely to be of West African origin, but could possibly have come from Moçambique on plant material carried by imported labour, although this seems most unlikely.

In April 1956, when the author visited Principe, there was a graded difference in the status of the scale from the north to the south of the island, with a considerable variation correlated with the location of individual trees. In the south, all the leaves of most trees were completely yellow due to scale attack, whereas in the north only the lower older leaves were yellow, the more recently formed leaves being very green and free from scale. The areas in between were intermediate in severity of attack. This reversal in the status of the scale since its introduction to, and southward spread from, San Antonio is attributed to the introduction of *Cryptognatha*. Coconut trees in sunny, exposed (both to sun and wind), dry situations are affected more severely by an attack than the average for that area; trees in sheltered positions, either in depressions or where they are protected by surrounding trees, may be very lightly attacked (possibly due to fungal attack on the scales). Trees in the latter situation, although they may show very little *Aspidiotus* attack, may, by reason of this position, yield very few nuts. These comparatively scale-free trees even occurred in the heavily attacked Infante D. Henrique area.

In April 1956 it was only in the south, at Roça Infante D. Henrique, that maximum active scale damage could be seen, and by July 1957 *Cryptognatha* had brought this well under control, the newly developing leaves being completely free from scale. In the north and centre in 1956, as stated above, the lower leaves of each tree were still quite yellow, whereas the upper half of the crown was quite green and virtually free from scale. In 1957, only the very lowest old leaves were yellow and in the rest of the crown there were only scattered isolated patches of scale, found rarely on individual pinnae. In fact the scale was well under control, and the trees had an appearance similar to those in Trinidad, W.I.

At Infante D. Henrique in April 1956, ten mature but not dying leaves were taken from ten different trees selected at random, and one of the tenth pinnae from the base of each leaf was examined. A one-inch-long section taken about

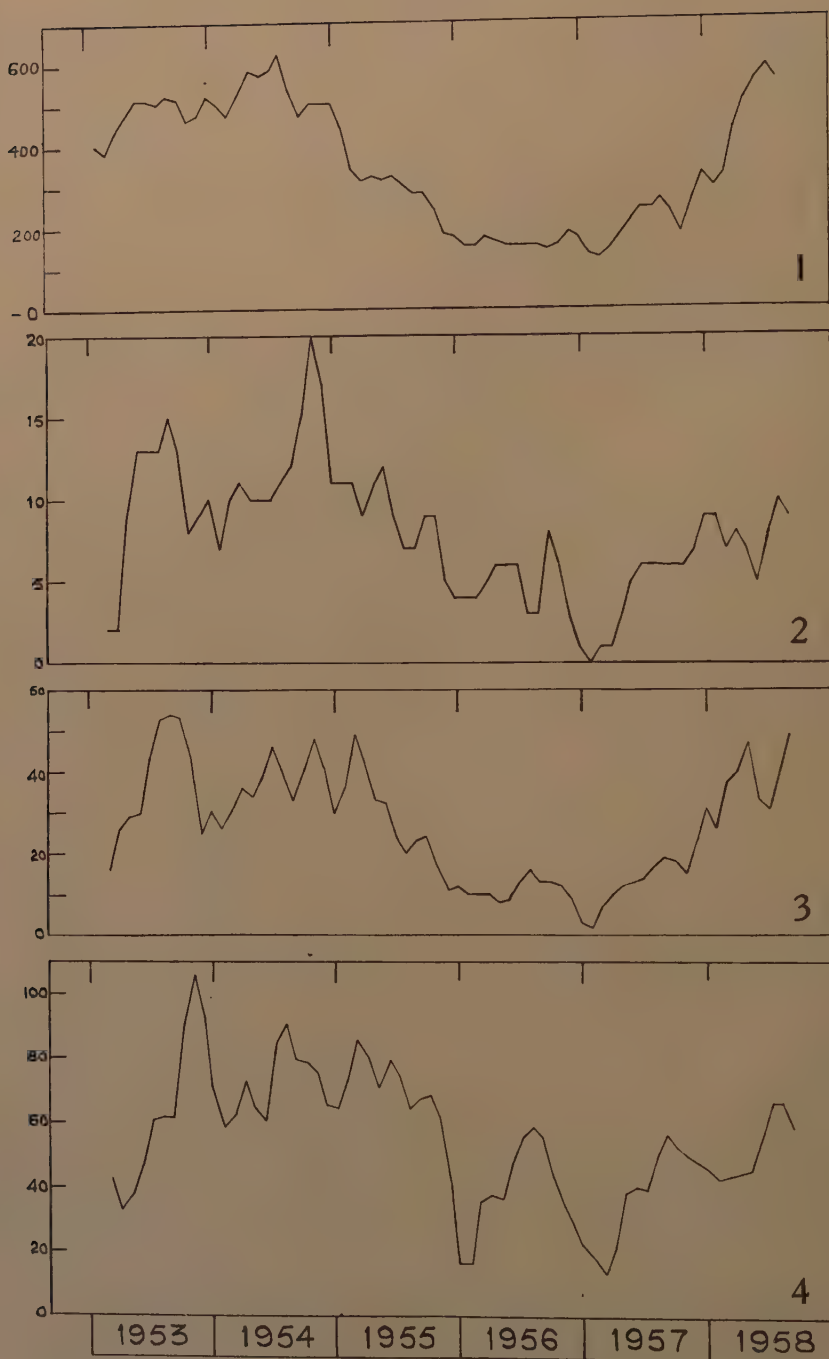
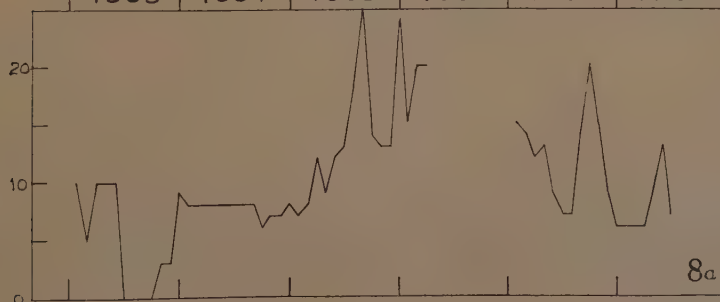
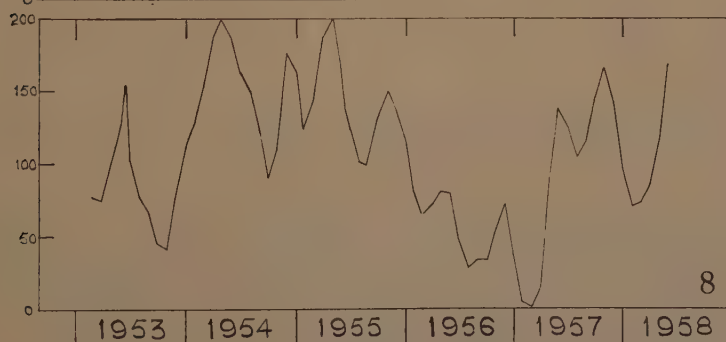
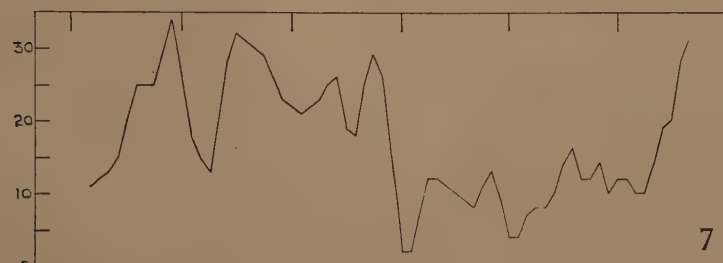
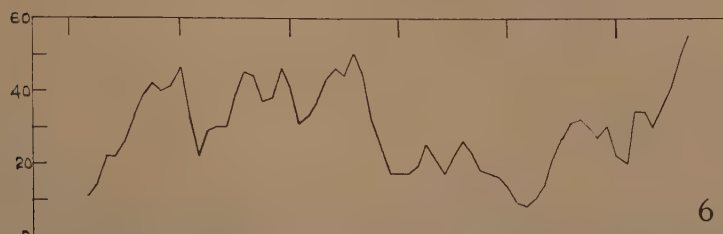
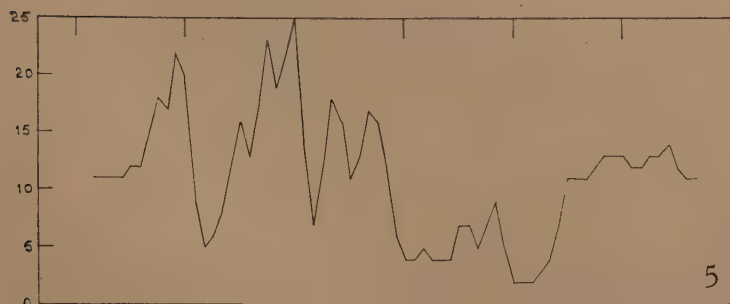


Fig. 3.—'Averaged' monthly data of copra production (in hundreds of kilograms) on eight estates in Principe, 1953-1958. (1) Sundy, (2) S. José, (3) Esperança, (4) S. Joaquim, (5) S. Carlos Fundão, (6) Anselmo Andrade, (7) Francisco Mantero, (8) Infante D. Henrique. Production of oil-palm kernels (in 100 kg.) on Infante D. Henrique (8a) is also shown (see text).



ten inches from its base was examined under a binocular microscope (see Table II). This showed that per inch of pinna on these leaves there was an average of about 207 mature, or nearly mature, females of *Aspidiotus* (maximum approximately 240, minimum approximately 160; absolutely accurate counting

TABLE II.

Populations of *Aspidiotus* on palm leaves, and dissection of 100 scales from each of ten trees. Numbers of scales per inch, and rates of parasitism and of attack by mites*. Roça Infante D. Henrique, April 1956.

Numbers of scales						
Tree	Count per inch of pinna	Not parasitised		Parasitised by <i>Aspidiotiphagus</i>		Parasitised by ectoparasite
		Total	Attacked by mite	Total	Attacked by mite	
1	160	16	4	84	26	—
2	240	83	31	15	5	2
3	210	48	21	51	19	1
4	240	88	20	12	5	—
5	190	22	8	78	29	—
6	240	26	9	74	21	—
7	200	78	30	21	4	1
8	210	39	15	61	18	—
9	180	12	3	88	24	—
10	200	19	4	81	20	—
Total	2070	431	145	565	171	4
Average	207	43.1	—	56.5	—	0.4
% attack by mites	—	—	33.6	—	30.1	—

**Hemisarcopetes malus*, a predacious species, of which total percentage attack was 31.6.

was difficult and was not regarded as essential under the circumstances). Comparable figures given by Castel-Branco (1956) were very similar. Each of these scales was producing from 50 to 80 eggs, and the potential numbers of crawlers per tree was therefore astronomical. Very young leaves developing in the crown of the tree were covered with crawlers, and developing leaves became covered with young scales at a very early age.

In other parts of the island, in 1956, where control of the scale by *Cryptognatha* was apparently most effective, it was difficult to find living scales, except for a few on younger leaves or under old dead scales, and consequently no comparable figures could be obtained. By 1957, as pointed out above, scale attack was in general reduced to the small patchy areas confined to a part of an individual or a few neighbouring pinnae.

In addition to coconut palm, *Aspidiotus destructor* was found on the fruit of the oil palm, *Elaeis guineënsis* (associated with *Lindingaspis opimus* (Silv.)), but not on the leaves. It was found on the leaves of the jack-fruit, *Artocarpus integer*, on *Aloe* sp. (an ornamental plant inside the hospital at Sundy), on cacao, banana and *Dianthus* sp.

Parasites and predators.

Castel-Branco (1956) mentions the presence of local unnamed Coccinellids preying on *Aspidiotus*, the parasites *Aspidiotiphagus citrinus* (Craw) and *Casca parvipennis* Gah., and scales killed by the fungus *Sphaerostilbe* sp. He gives figures for the mortality caused by each under different circumstances, but points out that they have not been able to check the catastrophic increase in the scale.

During April 1956, additional natural enemies were observed, parasites only being common in the southern part of the island where *Cryptognatha* had not yet developed its maximum effect. Predators seen were the Coccinellids *Endochilus styx* Sic. and ? *Orculus* sp. (a small Scymnine). In addition, the mite *Hemisarcoptes malus* (Shimer) was predacious on eggs of *Aspidiotus* under the scale shields, and destroyed very large numbers in some parts of the infestations. *Lasioseius* sp., another mite, was also found associated with these scales. Parasites of the scales were *Aspidiotiphagus lounsburyi* (Berl. & Paoli) (no example of *A. citrinus* was present in material sent for identification) and also a small yellow ectoparasitic species which was quite uncommon (0.4% of scales from the south). There was considerable fungal development on scales damaged by predators.

The results of dissections of *Aspidiotus* from trees selected at random at Roça Infante D. Henrique in the south are given in Table II. These scales were taken from the same material as was used to obtain an estimate of the scale density (see above). One hundred mature female scales were examined under a binocular microscope for parasitism by *Aspidiotiphagus* and the ectoparasite. The presence of *Hemisarcoptes* was also recorded. Parasitism by *Aspidiotiphagus* is seen to be very variable; moreover many of the parasitised scales containing living pupae of *Aspidiotiphagus* had already laid a considerable proportion of their eggs. Hence control of the scale population by this parasite is considerably less than might be expected from the percentage parasitism observed. Several leaves examined in areas in the south showed no signs of *Aspidiotiphagus*. In all samples, parasitism by the ectoparasite was negligible.

In the scale samples examined, 31.6 per cent. of the total had mites (*Hemisarcoptes*) under the shields, attacking the eggs. The proportion of eggs destroyed was not estimated, but destruction of potential crawlers must be considerable.

The numbers of Coccinellids present prior to the introduction of *Cryptognatha* may be roughly judged from Table III. The adults and larvae of both *Endochilus* and ? *Orculus* feed on *Aspidiotus*, but no quantitative data of the mortality caused was obtained. Castel-Branco (1956) gives 1.2–1.5 as the percentage destroyed in this way.

All parasites and predators, with the exception of *Cryptognatha*, must obviously be species which have other hosts in Principe, and which have only recently attacked *Aspidiotus*. A few observations were made on other hosts of these natural enemies. *A. lounsburyi* was also reared from *Pseudaulacaspis pentagona* (Targ.) on pawpaw (*Carica papaya*), from *Pinnaspis strachani* (Cooley) on *Erythrina* sp., and from an unidentified scale on cacao. The species also occurs in S. Tomé.

The mites *Hemisarcoptes malus* and *Lasioseius* sp. were found under egg-producing scales of *Pseudaulacaspis pentagona*, and *Hemisarcoptes* also under scales of *Hemiberlesia palmae* (Ckll.).

Endochilus styx was found commonly predacious on *P. pentagona*, and it might be noted here that two 'mummified' larvae of this Coccinellid were found with parasite emergence holes.

The status of *Aspidiotus* at Roça Infante D. Henrique in April 1956 was a clear indication that the control exerted by these local natural enemies was completely inadequate to prevent the development of an astronomical number of

TABLE III.
Numbers of Coccinellids present on leaves of different ages on five young coconut trees at Sundry, north coast of Principe, April 1956.

C = *Cryptognatha nodiceps*
A = *Endochilus styx*
B = ? *Orculus* sp.

Leaves, starting from centre of crown	Tree I			Tree II			Tree III			Tree IV			Tree V		
	Status of <i>Aspidiotus</i>	C	A B	Status of <i>Aspidiotus</i>	C	A B	Status of <i>Aspidiotus</i>	C	A B	Status of <i>Aspidiotus</i>	C	A B	Status of <i>Aspidiotus</i>	C	A B
1	None	0	0 0	None	0	0 0	None	0	0 0	None	0	0 0	None	0	0 0
2	None	0	0 0	None	0	0 0	None	0	0 0	None	0	0 0	None	0	0 0
3	None	0	0 0	Few	8	0 0	Few	5	0 1	None	0	0 0	None	0	0 0
4	Few	2	0 0	$\frac{1}{2}$ covered	60	8 18	$\frac{1}{2}$ covered	62	9 10	Few	2	0 1	Few	4	0 0
5	$\frac{1}{2}$ covered	53	6 4	v. heavy, dead	56	4 20	$\frac{1}{2}$ covered	57	2 16	Few	6	0 0	$\frac{1}{2}$ covered	41	1 5
6	v. heavy, dead	35	1 8	" "	50	7 8	v. heavy, dead	123	4 7	$\frac{1}{2}$ covered	35	4 7	v. heavy, dead	10	6 18
7	" "	42	2 20	Cut off			" "	31	3 6	v. heavy, dead	19	1 12	" "	19	1 12
8	Cut off						" "	7	0 2	" "	3	0 3	Cut off		
		132	9 32		174	19 46		285	18 42		65	5 23		74	8 35

All leaves older than the eighth had been cut off from all trees.

crawlers per tree, the speedy covering and debilitation of all leaves on most trees as soon as they develop, and the eventual reduction of nut production to practically nil on most trees. Undoubtedly, had no measures against *Aspidiotus* been taken, a large number of trees would eventually have died.

Effect of introduction of *Cryptognatha nodiceps*.

As pointed out, there was, in April 1956, a gradation from the south to the north of Principe from very active and severe attack by *Aspidiotus* to what appeared to be nearly complete control by *Cryptognatha*.

At Sundy and Bela Vista in the north, the trees were severely damaged and nut production was extremely low, but the trees were recovering. New leaves growing from the crown since about November or December 1955 had developed with little or no attack by *Aspidiotus* and were green and healthy. The appearance of the trees was peculiar. The three to five youngest leaves at the top of the tree were green, with little or no scale, the next oldest leaves had been partly attacked, and the remainder were completely yellow and dying prematurely due to the very heavy *Aspidiotus* attack that they had suffered. The scales were, however, nearly all dead on these oldest leaves. Five young trees were examined at Sundy to get an idea of the variation in numbers of *Cryptognatha*, *Endochilus* and ? *Orculus* sp. with different ages of leaf and on different trees. Only young trees were examined, since only on these could the leaves be inspected without disturbing adult Coccinellids. The older dead and dying leaves of many of these trees had been cut off. Each leaf, starting from the first expanded leaf at the heart of the crown, was examined, the degree of attack by *Aspidiotus* noted, and the numbers of the three species of Coccinellids on each leaf counted as accurately as possible. This was difficult since they moved, flew, or dropped off as the leaf was disturbed. Results are shown in Table III.

In this area there were between 65 and 285 *Cryptognatha* per tree examined, and about one-tenth and one-quarter of this number of *Endochilus* and ? *Orculus*, respectively. Both the last two species have been seen in themselves to be ineffective in controlling *Aspidiotus*. It is also noteworthy that fewer *Cryptognatha* were found on the lowest leaves bearing mostly dead scales, and very few on the scale-free young leaves. In this area at this time the numbers of *Cryptognatha* were extremely large, and most of the scale was dead or would shortly be killed. With the reduction of scale, numbers of *Cryptognatha* would be expected to decline, which is exactly what was found to have happened by July 1957, when in this area *Cryptognatha* was still widespread and common, but of the order of between 2 and 10 per tree.

It was in this area that attack was heaviest in September 1955, and here that the first releases of *Cryptognatha* were made. It was here, therefore, that biological control of the scale was likely to be attained first. However, recovery of copra production in this area was likely to be most adversely affected by the long dry season in 1955 since it is in the driest part of the island, and the trees may be affected for some considerable time. With regard to the effect, on the crop, of the scale, and its subsequent reduction by *Cryptognatha*, there were some indications seen in April 1956. There were, at Sundy, extremely few developing nuts older than 4-5 months (from flowering), and those of approximately this age were heavily covered with dead (eaten) scales. In the 2- to 4-month-old group, the number of nuts was only a small proportion of normal, but they were free from scale attack. The number of small nuts on the inflorescences was greater, but of course not all of these would reach maturity, since the general level of nutrition, dependent as it is partly on the state of the leaves, was only adequate for full development of a small fraction of the number set. There was, it was said, a noticeable improvement in the appearance of trees

from that shown 3-4 months previously. At that time nearly all the nuts were falling very prematurely, whereas at the later date very many more young nuts were remaining on the trees.

In July 1957 the trees had a very much more healthy appearance, and very many more nuts were developing on each. However, as is seen from fig. 3, actual copra production had only just started to recover, having remained at about 30 per cent. of pre-*Aspidiotus* normal since the end of 1955 when it had declined to its lowest level. By mid-1958, production was back to normal, indicating that biological control of the scale had been successful.

In the rest of the central area of the island, where there is more mixed cultivation, coconuts have not been so badly affected by *Aspidiotus*. *Cryptognatha* was found in all areas, was not generally common, but only so on occasional more severely attacked trees.

At Roça Infante D. Henrique, in the south-west coastal area, *Cryptognatha* had only been liberated since December 1955, and in March 1956 *Aspidiotus* attack was still generally very heavy, control being only in its initial stages, with numbers of *Cryptognatha* still increasing rapidly. Larvae and pupae were much more common than elsewhere, and individual coconut leaves were seen with patches of up to 200 pupae of *Cryptognatha*. This area is therefore probably some 4 to 6 months behind the northern part of the island with regard to the biological control of *Aspidiotus*.

Cryptognatha was found also commonly feeding on *Pseudaulacaspis pentagona* in most areas, and at Esperança it was common in 1956 on *Cycas revoluta* where it was feeding on *Hemiberlesia palmarum*.

A large number of larvae and pupae of *Cryptognatha* was examined but no case of parasitism was found. This is fortunate in view of the effect that parasites might have on the population of the species. As mentioned above, two parasitised larvae of *Endochilus* were found, and, in S. Tomé, larvae of *Chilocorus pilosus* Sic. were parasitised by *Tetrastichus* sp. near both *cydoniae* Risbec and *coccinellae* Kurd.

Discussion.

Since the introduction into Principe in August 1955 of *Cryptognatha nodiceps* there has been very spectacular control of *Aspidiotus destructor*. It is a pity that the scale was allowed to cause such devastation to the coconut trees before biological control was attempted, since the decline in copra production was considerable, and the trees sufficiently weakened for there to be a long lapse of time before recovery of production after the scale had been brought under control.

It had been claimed that on the north coast of Principe a number of coconut trees had been killed by *Aspidiotus*. This was investigated, but in general the claim cannot be substantiated. Had the scale been allowed to progress unchecked it is very probable that a number of trees would have died in time, but those that had died by 1956 were either very old trees, those that had suffered other forms of damage, or were growing under extremely poor soil and water conditions. Before the attack of *Aspidiotus* they were in very poor condition, bearing very few nuts, and while the damage caused by the scale might have been sufficient to administer the 'coup de grace', they were already either dying trees or else completely unthrifty, and the scale did not in fact cause any economic damage in removing them.

The introduction of *Aspidiotus* into Principe has obviously caused a catastrophic reduction in the copra crop, but it should be remembered that there are a number of other factors that affect the yields. The influence of climate, particularly rainfall, soil, drainage, variety of palm, etc., is obvious. In mixed cultivations where coconuts are grown along with other crops such as cacao, oil palms or

coffee, copra yields will tend to be lower. Several coconut areas in Principe appear to be semi-abandoned or very ill-kept. Owing to the competition by the undergrowing bush for soil water and nutrients, these areas give reduced yields, the amount of this reduction depending naturally on the quality of the soil and the growth of the bush.

There are also several biotic factors affecting copra production in Principe. In addition to *Aspidiotus* there are several other scales found on coconut leaves: *Ischnaspis longirostris* (Sign.) is common, but not abundant, *Selenaspis articulatus* (Morg.) has been recorded, *Hemiberlesia palmae* is fairly common, and *Vinsonia stellifera* (Westw.) is widespread but never common. These quite obviously cause comparatively little damage, and some may have been attacked by the local natural enemies now attacking *Aspidiotus*.

Some coconut trees have their crowns attacked by an adult Dynastid which was not seen, and damage is in fact comparatively rare.

Two pests of an entirely different nature are monkeys and rats. Monkeys (*Cercopithecus mona mona* (Schreber)) were introduced from West Africa, and numbers occur in the forested areas. These cause serious losses in coconut plantations (and in cacao too) since they pick off a large number of small and medium-sized nuts, most of which they cannot eat, and throw them to the ground. They are particularly destructive, naturally, in coconut areas bordering on the forest.

Rats are a very serious pest of both coconuts and cacao in Principe, and a widespread campaign using 'Warfarin' has been carried out. Nevertheless the numbers of young nuts destroyed by rats is very considerable. It is possible that biological control may play a part in this problem. In the neighbouring island of S. Tomé, rats are not a serious problem, and in the plantations there occur numbers of the scavenging kite, *Milvus migrans* (Bodd.), which are said to feed on, amongst other things, rats. These birds are very uncommon in Principe and are rarely seen in plantations. It is said that they are 'mobbed' by the grey parrot, *Psittacus erithacus* L., which is very common. It would be interesting to know if a serious reduction in the numbers of parrots would lead to an increase in the population of kites with an ensuing decrease in the number of rats.

A comparison may be made between the state of the coconuts in Principe and that in S. Tomé, where *Aspidiotus* is not present. Other scales are present on the leaves on this latter island, but patches of yellowing are only found irregularly on several pinnae of mature leaves (as in other coconut-growing areas where *Aspidiotus* may be present but under reasonable control). Of the complex of scales attacking coconut leaves in S. Tomé the most important is *Hemiberlesia palmae*. Also present are *Ischnaspis longirostris*, ? *Lepidosaphes* sp., *Selenaspis articulatus* and *Vinsonia stellifera*—very similar to the complex in Principe without *Aspidiotus*. However, the predator situation is very different (parasites of these other scales were not investigated, but *Aspidiotiphagus lounsburyi* is present in S. Tomé). *Endochilus styx* is not present, but there is an *Orculus* sp., possibly the same as that in Principe; other Coccinellids present with scales on coconut leaves in S. Tomé are *Chilocorus pilosus*, *Endochilus plagiatus* Sic., *Exochomus flavipes* (Thnb.) and *Pharoscymnus* sp., ? *exiguus* (Weise). This complex is entirely different from that in Principe, and it is possible that if *Aspidiotus destructor* did become established in S. Tomé these predators might be able to control it effectively.

Cryptognatha has been able to control *Aspidiotus* very satisfactorily in Principe, but it is certain that the pest will not be exterminated, and whether or not the introduction of additional species of Coccinellids should be considered in the future depends on the over-all long-term degree of control effected by *Cryptognatha*. As the population of *Aspidiotus* is reduced, that of *Cryptognatha* will decline until

it may become generally uncommon, only being found in small temporary outbreaks of *Aspidiotus* which are almost bound to occur in the future. However, the fact that *Cryptognatha* can maintain a population also on *Pseudaulacaspis pentagona* on pawpaw, etc., and on *H. palmae* on *Cycas* (it had reduced attack by this scale considerably at Esperança by July 1957) will help in preventing numbers of this Coccinellid from declining too much even if *Aspidiotus* is reduced to a very low level.

It is possible, even if control by *Cryptognatha* continues to be adequate, that there will be seasonal fluctuations in attack by *Aspidiotus*, which would be more plentiful at the end of the dry season, and it is probable also that the damage caused will eventually be somewhat higher on the drier northern coast than on the rest of the island. Keeping trees in a thrifty condition will keep scale damage to a minimum, and trees growing in poor soil, in exposed situations, or in overgrown plantations, are likely to show heavier attack than those growing under favourable conditions.

It can certainly be claimed that the introduction of *Cryptognatha nodiceps* into Principe against *Aspidiotus destructor* is a recent outstanding example of effective biological control, and Dr. Castel-Branco is to be congratulated on the organising of this campaign and the mass breeding and release of large numbers of *Cryptognatha*. It is seldom that adequate data are available to indicate clearly the economic benefits derived from the introduction of a natural enemy of an insect pest, but from the data on copra production shown above it is in this instance very definite. The gradual decline in copra production and its subsequent recovery are clearly shown, various areas differing in this regard for the reasons explained above.

Summary.

The coconut scale, *Aspidiotus destructor* Sign., was recorded for the first time from the island of Principe in November 1954, but it is practically certain that it was actually introduced accidentally in 1952.

Prior to 1954, normal fluctuations had occurred in the total annual production of copra of the island, probably correlated mainly with rainfall conditions. However, in 1954 there was a steady and very serious decline in production due to damage caused by *Aspidiotus*. Several species of endemic natural enemies were found attacking the scale, but the control exerted by them was quite inadequate to prevent astronomical increase of *Aspidiotus*.

The predacious Coccinellid, *Cryptognatha nodiceps* Mshl., was introduced into Principe from Trinidad, W.I., in August 1955. The course of spread of both scale and predator are traced and the effect that each has had on the production of copra is shown.

There is a considerable time lag between the incidence of heavy scale attack, or its control, and the effect on yields of copra. Even though complete economic control of the scale had been obtained by July 1957, copra production only recovered to its pre-scale level by the middle of 1958, three years after the introduction of *Cryptognatha*.

Cryptognatha was also found feeding on other species of scales on different host-plants. No parasitism of larvae or pupae of *Cryptognatha* was observed, although parasites of the larvae of endemic Coccinellids were recorded in both Principe and S. Tomé.

Biotic factors other than *Aspidiotus* affecting copra production are mentioned, the most important being monkeys and rats, and a comparison is made between the situation of scale insects in general on coconuts in Principe and that in S. Tomé where, as yet, *Aspidiotus destructor* does not occur.

Acknowledgements.

I should like to express my thanks to the various members of the Commonwealth Institute of Entomology and staff of the British Museum for identifications of material mentioned here.

References.

- CASTEL-BRANCO, A. J. F. (1956). A cochonilha dos coqueiros na Ilha do Príncipe (*Aspidiotus destructor* Sign.).—*Garcia de Orta* **4** pp. 225–238.
- CASTEL-BRANCO, A. J. F. (1959). Lutte biologique contre *Aspidiotus destructor* Sign. à l'île Príncipe (Afrique-Occidentale Portugaise).—*Rev. Path. vég.* **37** pp. 235–239.

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A NEW SPECIES OF *DYSMICOCOCCUS* FERRIS (PSEUDOCOCCIDAE,
HOMOPTERA) ON BANANA.

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R

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The following species taken in London on imported bananas has been submitted recently for identification and has proved to be a new species of *Dysmicoccus* Ferris.

On checking some unidentified material in the British Museum (Natural History), the same species has come to light on imported bananas collected in London earlier. As some of these were labelled "from Canary bananas", a check was made of all the material in the British Museum (N. H.) of mealybugs from the Canary Islands and it is evident that the species is widespread there but has been misidentified as *Pseudococcus comstocki* (Kuw.). Furthermore, it has been misidentified as this species on other occasions on imported bananas in England and Egypt and although some of the preparations concerned are labelled as from Canary bananas, it is not possible to determine whether all have come from this source.

Specimens at hand from cactus in the Canary Islands were probably obtained from that plant as a result of their falling from the banana plants. The species may be found in other banana-growing areas but Dr. W. J. Hall has informed the writer that during seven years in Egypt he had not collected it on bananas growing in that country.

The holotype and paratypes are deposited in the British Museum (Natural History).

***Dysmicoccus alazon*, sp. n. (fig. 1).**

Habit. At present known only as associated with the fruits of bananas. External appearance not known.

Recognition characters. An oval species measuring approximately 3 mm. long. Antennae 8-segmented. Legs rather long and slender, the hind femur and tibia with numerous translucent pores. Circulus present, well developed with a distinct fold. Anal ring normal, with 6 setae about twice as long as its diameter. Ostioles with 2-4 setae on each lip and with inner edges of lips sclerotised. Cerarii numbering 17 pairs; anal lobe cerarius with 2 long, conical setae surrounded by a number of trilocular pores which are not crowded and also about 5 slender setae all enclosed in an ovoid sclerotised area; anterior cerarii smaller, each comprising a pair of conical setae or 3 on the head region, accompanied by a cluster of trilocular pores and 3-5 slender auxiliary setae and surrounded by a small sclerotised area. Dorsal pores of trilocular type only, evenly distributed.

Ventral surface with a short sclerotised area on each anal lobe and an apical seta about the same size as anal ring setae. Ventral setae slender but longer than those on dorsum, not numerous. Multilocular disc pores confined to segments posterior to circulus although an occasional pore often present on fourth segment; arranged in single transverse rows at posterior edges of fifth and sixth segments and in more or less double rows at posterior edges of seventh and eighth segments, present also in single rows at anterior edges of sixth to eighth segments and in a dense cluster posterior to vulva. Tubular ducts of oral collar type

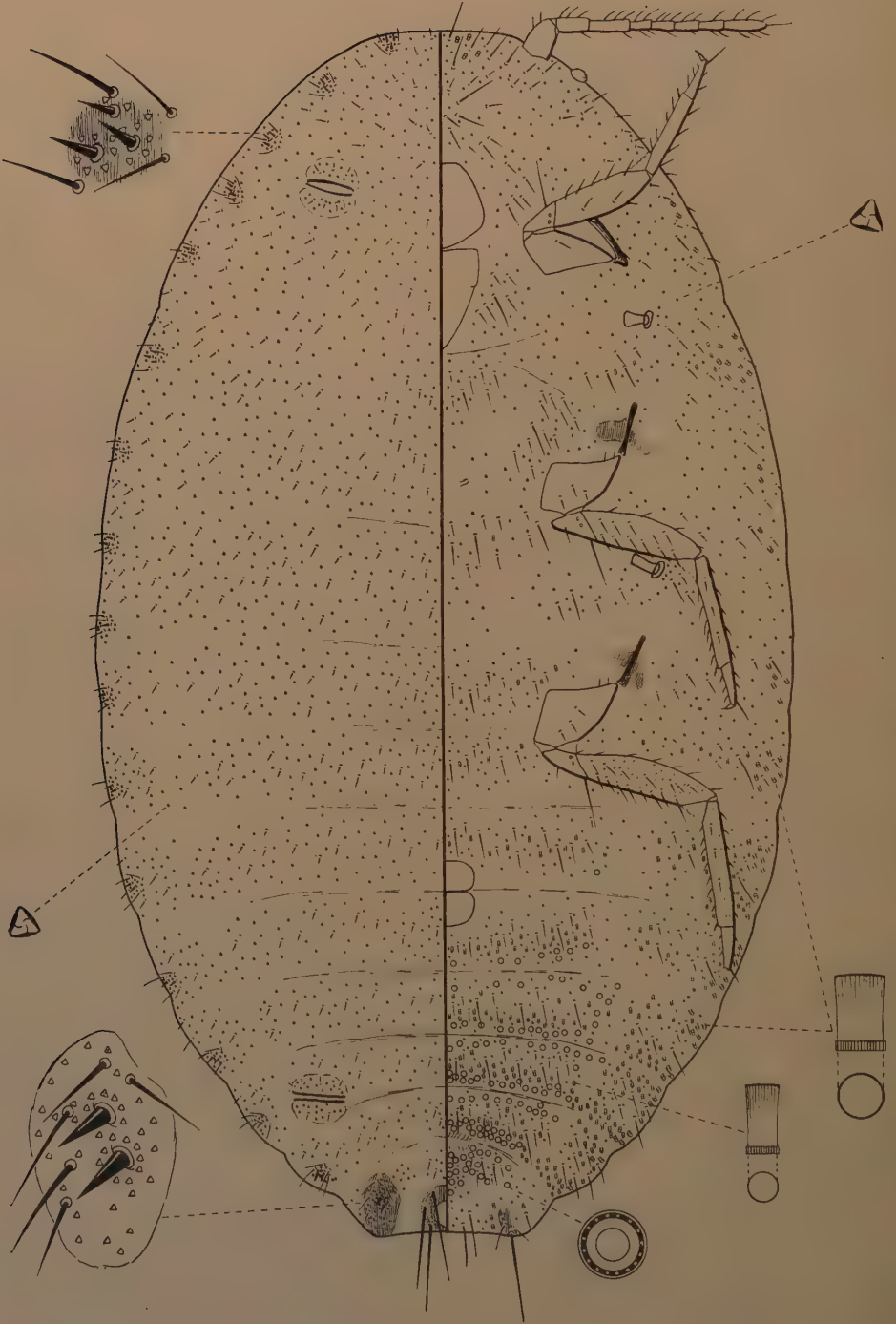


Fig. 1.—*Dysmicoccus alazon*, sp. n.

present in two sizes; a smaller type rather numerous on abdomen in transverse rows and also around the anal lobes and in submarginal groups, a few others in midregion of thorax and in a submarginal group on mesothorax; a larger type of duct present in noticeable marginal groups from the seventh segment anteriorly to head. Trilocular pores evenly distributed, not numerous.

Described from the following material:—

CANARY ISLANDS: No locality, 27.x.1924; Hoyo Grande, no data; Las Palmas, 10.viii.1924 (*V. C. Dunlop*); Arucas, on cactus, 9.viii.1924 (*V. C. Dunlop*).

ENGLAND: Camberley, December 1916, 10.xii.1920 (*E. E. Green*); London, 12.v.1927 (*F. Shaw*); 31.viii.1927 (*A. H. Ritchie*); 20.ix.1958 (*R. H. Harris*) (Holotype); October 1958 (*P. Brodie*). All on imported bananas.

EGYPT: Alexandria, 25.xii.1919, 25.xii.1923, 6.ii.1925; Cairo, 26.i.1922 (*W. J. Hall*). All on imported bananas.

Notes. Because of the absence of oral rim ducts this species is excluded from the genus *Pseudococcus* Westwood but in general appearance and especially in the arrangement of the ventral multilocular disc pores and the anal lobe cerarii it resembles *Pseudococcus comstocki* (Kuw.), with which it has been misidentified. Of the species so far assigned to the genus *Dysmicoccus*, it comes closest to *D. aciculus* Ferris, described from California on *Pinus radiata*, but the latter species lacks a circulus and has much fewer multilocular disc pores.

THE EFFECT OF A RESIDUAL HOUSE-SPRAYING CAMPAIGN IN EAST AFRICA ON SPECIES BALANCE IN THE *ANOPHELES FUNESTUS* GROUP.

THE REPLACEMENT OF *A. FUNESTUS* GILES BY *A. RIVULORUM* LEESON.

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L.B.

The Taveta-Pare Malaria Control Scheme was intended to test the effects of residual house spraying with dieldrin on the transmission of malaria in an inland region of Kenya and Tanganyika. Detailed accounts of malaria transmission and of the first results of this campaign have already been published, Draper & Smith (1957), Smith & Draper (1959). In addition to observations on the effects of immediate importance in public health, studies were made of the behaviour and of the changes in population numbers of the vector mosquitos, *Anopheles gambiae* Giles and *A. funestus* Giles, induced by the application of insecticides. In planning these studies, the possibility was borne in mind that the selective destruction of house-haunting vectors might give rise to changes in the numbers of other species. An earlier example of such a change was reported by Trapido & Aitken (1953) in Sardinia, where the elimination of *Anopheles labranchiae* Flin. led to an enormous increase in *A. hispaniola* (Theo.). In the Taveta-Pare Scheme, artificial shelters were extensively used to assess the outside resting population and, in addition to counts of the main vectors, records were kept of the catches of other species of *Anopheles*. Thus we were in the unusual position of being able to follow the changes in density of certain species that were initially less common, over a period that extended from one year before to three years after the inception of residual house spraying.

The present paper is devoted to the question of species balance in the *A. funestus* group, which is represented in the Taveta-Pare area by the house-resting *A. funestus* (s. str.), by *A. funestus* var. *confusus* Evans & Leeson and possibly by other less well defined forms and by the exophilous species *A. rivulorum* Leeson. We record here the changes in species balance observed in South Pare district, where the apparently complete elimination of typical *A. funestus* was accompanied by a dramatic increase in the density of *A. rivulorum*.

Technique.

The clearest evidence of changes in the relative densities of *A. funestus* and *A. rivulorum* was provided by catches made in box-shelters, of the type described by Gillies (1954), set up in and around the village of Kihurio in the South Pare district of Tanganyika. Mosquitos were particularly abundant in this village at certain seasons, owing to the widespread use of irrigation and the cultivation of rice. Catches in the boxes were consequently also high, their effectiveness as a collecting method being enhanced in this area by the semi-arid nature of the vegetation and the resulting paucity of natural resting sites.

The box-shelters were set up in three sectors: along the banks of an irrigation channel running through the middle of the populated area; on the edge of the

TABLE 1.
Catches of females of *A. funestus* and *A. rivulorum* in box-shelters at Kihurio before spraying.

	Total numbers caught		Estimated numbers of unrecognised <i>A. rivulorum</i>	Corrected catch*		No. of catches (box/days)	Corrected catch per 20 box/days	
	<i>A. funestus</i>	<i>A. rivulorum</i> ('two-spot' females only)		<i>A. funestus</i>	<i>A. rivulorum</i>		<i>A. funestus</i>	<i>A. rivulorum</i>
May 1954	623	24	12	611	36	65	188	11.1
July 1954	531	107	53.5	477.5	160.5	375	25.5	8.6
Oct. 1954	40	10	5	35	15	288	2.4	1
Jan. 1955	30	0	0	30	0	230	2.6	0
April 1955	349	24	12	337	36	230	29.3	3.1
July 1955	111	35	17.5	93.5	52.5	230	8.1	4.6
Oct. 1955	82	11	5.5	76.5	16.5	230	6.6	1.4

Houses first sprayed November 1955.

* Corrected by subtraction of the estimated numbers of unrecognised *A. rivulorum* from the catch of *A. funestus*; and by addition of the same estimate to the catch of 'two-spot' *A. rivulorum*.

village; and in the vicinity of the rice-fields at a distance of a half to three-quarters of a mile from the nearest houses. Initially 25 boxes were set up. Two fell into disuse during the first year, but the remaining 23 boxes survived, in varying degrees of repair and replacement, throughout the four and a half years' observations. At times the crumbling away of the earth mounds built up round the boxes and the tearing of the curtains may have temporarily altered their attractiveness to mosquitos. There were also occasions when a number of curtains disappeared between visits, and when this occurred the catches were usually not recorded until fresh curtains were in position. But on the whole the total array of resting sites offered to mosquitos remained the same throughout the period. It should be added that, with the possible exception of the last season, no major

TABLE II.

Catches of females of *A. rivulorum* in box-shelters at Kihurio after spraying.

Month	1956		1957		1958	
	Numbers caught	Nos. per 20 box/days	Numbers caught	Nos. per 20 box/days	Numbers caught	Nos. per 20 box/days
January	0	0	37	4.8	9	1.5
February	—	—	34	3.1	20	2.3
March	—	—	38	5.3	56	4.3
April	437	67.7	143	31.8	133	17.6
May	245	42.2	549	<u>109.8</u>	264	<u>31.8</u>
June	323	35.5	397	60.2	59	9.5
July	36	4.2	154	27	40	4.9
August	—	—	—	—	30	3.4
September	5	4.2	25	5.6	4	0.5
October	13	1.8	3	0.6	1	0.2
November	0	0	6	0.9	0	0
December	3	0.3	3	1.1	0	0

alterations in the housing areas or in the timing or extent of irrigation took place. Thus these outdoor catches were maintained more or less regularly in the same boxes in the same way during the eighteen months before, and for three years after, the first application of insecticide to houses.

Mosquitos were collected from the shelters in the morning, using test tubes or suction tubes. In the pre-spraying period, catches were made on 10–15 days during every third month. After the spraying, catches were made much more frequently. Only female mosquitos were counted. The bulk of those caught in the initial period were *A. gambiae* and *A. funestus*, together with small numbers of *A. rivulorum* and occasional specimens of other species of *Anopheles*. The adults of *A. rivulorum* could not, at that time, be distinguished from those of the much more numerous *A. funestus* unless they had a second pale patch of

scales on the upper branch of the fifth vein. This character is always absent in *A. funestus*, but it is present in *A. rivulorum* to an extent which appears to vary with the locality. In the Pare district, observations made since the spraying have shown that about two-thirds (67.5 per cent. of 763 examined) of females of *A. rivulorum* carry this distinguishing marking. Such females may conveniently be termed 'two-spot' *rivulorum*. In sorting the catches, a separate record was kept of all 'two-spot' females, and their identity was confirmed in many instances by examination of the eggs.

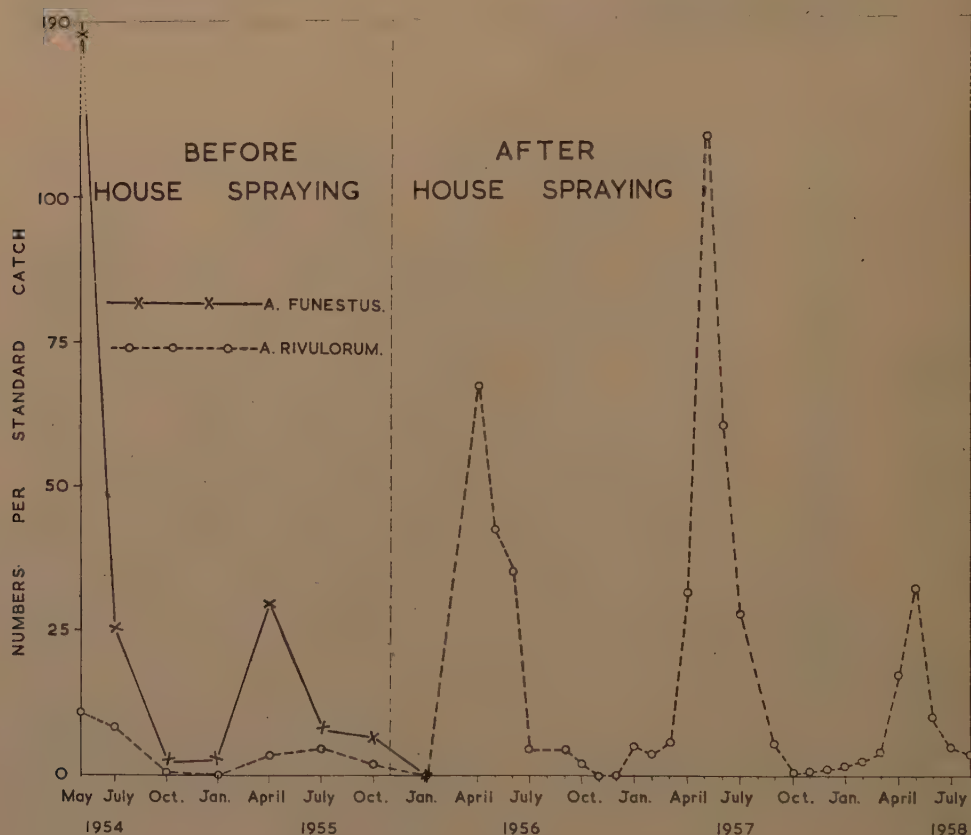


Fig. 1.—Effect of residual house spraying on populations of *A. funestus* and *A. rivulorum*, as shown by catches in artificial outdoor shelters.

As well as the catches made in box-shelters at Kihurio, information was obtained from house catches, by larval surveys, by the use of box-shelters in other areas, and by catches at night on human bait. In the latter two instances, however, separation of *A. rivulorum* from *A. funestus* was not always attempted during the pre-spraying period. The same applies to the catches recorded in Tables III and IV. The house catches were made in the course of routine spray-sheet collections throughout the South Pare district, the detailed results of which have already been described by Draper & Smith (1957). These authors also give a sketch map of the district, which shows the relationship of Kihurio to the district in general and to the swamp villages, mentioned elsewhere in this paper.

Changes in the densities of *A. funestus* and *A. rivulorum*.*Catches in outdoor shelters.*

The results of catches of *A. funestus* and *A. rivulorum* at Kihurio during the years 1954-1958 are shown in Tables I and II. The right-hand column in each table gives the average monthly catch expressed as numbers per "20 box/days." The number of boxes in use on any particular day and the number of catches in a month varied slightly. Twenty box/days represents approximately one day's catch and has accordingly been chosen as a useful standard for comparison. From Table I it will be seen that *A. funestus* was seasonally abundant in 1954 and 1955 up till the time of the first spraying. Thereafter the species virtually disappeared from the catches, and the last specimen to be identified with certainty as typical *A. funestus* was caught in January 1956.

From the same tables and from fig. 1, in which the same data is presented, it is seen that catches of *A. rivulorum* were low at all seasons prior to the house spraying. Following the spraying, and in parallel with the disappearance of *A. funestus*, a striking increase in the density of *A. rivulorum* took place. The density curve has a marked seasonal form, catches being high from April to June or July and low during the rest of the year. In the three years after spraying, peak densities ranged from 32-110 per standard catch, while in 1954 and 1955 under the same conditions not more than 11.1 and 4.6 females were caught. If one compares the peak months of April and May in the two pre-spraying years taken together (7.1) with the combined average for these months in later years (50.1), an increase of about seven times the previous population level is shown.

TABLE III.

The average numbers of *A. funestus* and *A. rivulorum* caught per man/night between 1900 and 2100 hr. at Gonja.

	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
1954-55 Before dieldrin : <i>funestus</i> group	0	2.2	0	0.1	0.5	4.4	2.8	0.9	1.7	0.4	0	0
1955-56 After dieldrin : <i>funestus</i>	0	0	0	0	0.6*	0	0	0	0	0	0	0
<i>rivulorum</i> ..	0	0	0	0	—	3.9	5.7	0.9	0	0.1	0	0
1956-57 <i>rivulorum</i> ..	0	0	0.7	0.4	1.2	2.5	6.5	3.6	0.1	0	0	0
1957-58 <i>rivulorum</i> ..	0.1	0	0.7	0.3	0	0.2	1.3	1.0	0.7	0	0	0

* *funestus* group.

Catches off human 'bait.'

The high densities of *A. rivulorum* after residual spraying, as shown by collections in outdoor shelters, is reflected in catches off human bait. Determinations separating *A. rivulorum* and *A. funestus* were introduced into routine catches in April 1956, and specimens of *A. rivulorum* were subsequently distinguished

either by wing characters or by thoracic colouring (in fresh specimens the integument generally has an orange tinge). It can be seen from Table III that the peak incidence is in April to June which, as shown by Draper & Smith (*op. cit.*), corresponds to the seasonal peak of abundance for *A. funestus* in the Pare area. The significance of this fact is referred to later (p. 250). During the third year after spraying, catches were considerably lower.

TABLE IV.

Average numbers of *A. funestus* and *A. rivulorum* per hut in villages near swamps in South Pare district.

	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
1954-55												
Before dieldrin : <i>funestus</i> group	61	9	7	13	19	65	47	67	43	41	19	12
1955-56												
After dieldrin : <i>funestus</i> group	1.4	0	0	0.02	0.08	0.09	0.03	0	0	0	0	0
<i>rivulorum</i> ..	—	—	—	—	—	0.26	0.39	0.22	0.06	0	0	0
1956-57												
<i>rivulorum</i> ..	0	0	0.06	0	0.06	0.26	0.16	0.37	0.38	0.12	0.03	0.03
1957-58												
<i>rivulorum</i> ..	0	0.01	0.17	0.09	0.07	0.59	0.1	0.32	0.2	0.07	0.02	0.03

House catches.

During the pre-spraying period, house catches consisted almost exclusively of *A. gambiae* and *A. funestus*. As shown in Table IV, large numbers of individuals of the *funestus* group were caught in villages in the swamp area of South Pare district. *A. rivulorum* was always scarce in houses in the day-time, and before the spraying no attempt was made in routine catches to separate the different members of the *funestus* group. Soon after the first round of spraying, typical *A. funestus* disappeared from houses, but despite the abundance of *A. rivulorum* in outdoor shelters at Kihurio the monthly average of females caught

TABLE V.

Densities of *A. rivulorum* (females) as shown by spray catches in houses after dieldrin treatment.

	First year Apr.-Oct. 1956	Second year Nov. 1956-Oct. 1957	Third year Nov. 1957-Oct. 1958
Swamp villages			
No. houses ..	442	834	1007
No. <i>rivulorum</i> ..	59	121	131
Av. per house ..	0.13	0.15	0.13
Main road			
No. houses ..	628	1028	923
No. <i>rivulorum</i> ..	25	48	46
Av. per house ..	0.04	0.05	0.05

per treated house in swamp villages ranged from 0 to 0.39 during the subsequent three years. If the total number of females of *A. rivulorum* caught in each year be divided by the number of treated houses examined, the annual average per house is found to be not more than 0.13–0.15. These figures are for swamp villages, with which, rather than with the main-road villages, Kihurio has more in common (see below). The annual average for the main-road villages was 0.04–0.05. These annual catches are shown in Table V.

In 214 catches in untreated houses, examined during the same period, an average of 0.6 female of *A. rivulorum* per hut was collected.

Feeding preferences.

As already reported by Draper & Smith (1957), *A. funestus* in the Taveta-Pare area was a highly anthropophilous insect. *A. rivulorum*, on the other hand, is mainly zoophilous. The results of precipitin tests on gorged females of this species found in outdoor shelters in the day-time are shown in Table VI. It will

TABLE VI.

Results of precipitin tests on *A. rivulorum* caught in day-time shelters.

Site	Number of smears positive for						Total
	Man	Man/ox	Ox	Sheep or goat	Dog	Others (including negatives)	
Kihurio boxes ..	12	1	413	26	7	75	534
per cent. ..	2.2	0.2	77.3	4.9	1.3	14.1	
Gonja boxes	6	—	4	7	1	4	22
Houses :							
Near swamps ..	1	—	27	5	—	1	34
Near main road	8	—	8	7	—	4	27
Eaves	—	—	16	3	—	—	19

be seen that the great majority of captures had fed on cattle. The rather higher proportion, that had fed on man, among the small sample from box-shelters at Gonja and from houses in the 'main road' area of South Pare district, almost certainly reflects the relative absence of domestic animals in these particular villages. Cattle are kept in some numbers in the roadside village of Kihurio because it lies near the swamps and grazing areas of the Mkomazi valley, due to a curvature in the Mkomazi river. Watering places are also available at the Sasseni river on the side of the road nearer the Pare Mountains. In areas between Gonja and Ndungu (see Draper & Smith, 1957, p. 138) nearly all cattle are penned near the swamps which are about two miles from the roadside villages.

Discussion.

Sources of error.

From the description of the box-shelter catches at Kihurio, it should be clear that we were collecting comparable samples of the *A. rivulorum* population before

and after spraying. It is also evident, from the catches made in three successive years, that the increase in the population was relatively permanent and not simply the result of abnormal weather conditions during a single season. Densities in the third year after spraying were certainly lower than in the two previous seasons, but they were still three times greater than the peak pre-spraying catch (that for May 1954). It should also be emphasised that, while there was some extension of the areas under irrigation in the South Pare district generally, there was no major change in the Kihurio area and none that could have more than a minor effect on mosquito breeding.

In connection with the identification of the material, it is possible that the mosquitos were examined more closely after spraying than before, a factor which might tend to exaggerate the differences observed. There might also have been changes in the proportion of *A. rivulorum* with 'two-spot' wing markings during the period of the observations. Nevertheless, in comparison with the possible effects of these minor factors, the increase in density after spraying was so striking that there can be little doubt but that the changes were genuinely associated with the spraying; and it is suggested that they may be directly related to the elimination of *A. funestus* through residual house spraying.

Biological factors.

In blood-sucking insects, the success of individuals in obtaining food is seldom influenced by their numbers, except possibly when the host is virtually overwhelmed by their attacks. In the present instance, the specific differences in choice of host make it even more unlikely that there could be any interaction between the adults of *A. funestus* and *A. rivulorum*. Consequently the reasons for the dramatic rise in density of the latter species must be looked for in the aquatic phase of life, a subject on which we have very little information.

In the preliminary survey, it was found that considerable proportions of the larval populations of both species were found together in the same breeding sites. The overlap is not complete, however, for *A. rivulorum* colonises sites with more rapidly moving water than *A. funestus* and tends to avoid small bodies of standing water. In the South Pare area, flooded rice-fields and irrigation channels would be the principal breeding places of both, and interspecific competition might well take place. Following the disappearance of *A. funestus* after the spraying, we found no evidence of *A. rivulorum* spreading out and colonising ponds and stagnant waters. Hence it seems reasonable to conclude that competition with *A. funestus* within its normal habitats was responsible for the relative scarcity of *A. rivulorum* under natural conditions. The fact that the seasonal peaks of abundance of the two species coincide has already been mentioned on p. 248. This is significant because it could accentuate such competition.

Up to now, consideration has only been given to the presumed interaction of *A. funestus* and *A. rivulorum*. The assumption that other species were not involved needs examination. *A. gambiae* was the most abundant mosquito in houses and outdoor shelters before the spraying commenced. Catches in later years in the Kihurio boxes and in houses in comparable areas never exceeded 25 per cent. of the pre-spraying figures, and for much of the year the catches were relatively lower still.

During the initial larval survey, *A. gambiae* was found to be present in 7 out of 14 breeding sites of *A. rivulorum* examined. These sites were mainly in the grassy margins of streams, and, although the larvae of the two species may not have been in close contact, it could be postulated that there was at least some interaction between them. However, the annual peak for *A. gambiae* lay early in the wet season, during the months of January to March, while the production of *A. rivulorum* was always at its greatest from April to May. Hence it seems

likely that the most important factor influencing the production of *A. rivulorum* was the elimination of *A. funestus* from its breeding sites, although the importance of the reduction in the numbers of *A. gambiae* cannot be entirely dismissed.

Epidemiology.

The implications of this situation in terms of malaria transmission were actively studied. It was shown, for example, that *A. rivulorum* exhibits a well marked tendency to feed out of doors. Catches made on human bait, during four nights in April 1956, yielded a total of only 2 females inside houses, while 127 were caught outside; and at certain times and places, after the spraying, it had become the commonest mosquito biting man outside. Only a small series of gland dissections was made, and of 66 dissected before, and of 172 after the spraying, none was positive for sporozoites. Such a short series of dissections would, of course, be unlikely to disclose the occasional specimen that had acquired an infection and survived to transmit malaria.

More valuable evidence comes from studies on the host choice of this species which, as already shown, is predominantly zoophilous. It appears that, in the presence of cattle, *A. rivulorum* is a harmless mosquito, preferring animal blood when available, and only turning to man when other hosts are absent. Although the data are not wholly conclusive, it seems unlikely that this change in species balance has interfered with the operation of malaria control.

Summary.

In the course of an experiment in malaria control in an inland region of Kenya and Tanganyika, by the use of house spraying with dieldrin, routine catches were maintained of mosquitos resting in artificial outdoor shelters. During the 18 months of the pre-spraying period, catches in the South Pare district of Tanganyika mainly consisted of the principal vectors, *Anopheles gambiae* Giles and *A. funestus* Giles, together with small numbers of *A. rivulorum* Leeson.

During the three years following the spraying, *A. funestus* disappeared almost completely from the catches, while *A. rivulorum* showed an increase of about seven times above its former level.

It is concluded that this change in numbers of *A. rivulorum* was associated with the disappearance of *A. funestus* from breeding sites formerly occupied by both species.

Precipitin tests indicated that *A. rivulorum* is mainly zoophilous and had not played any part in malaria transmission.

Acknowledgements.

We would like to express our gratitude to Dr. D. Bagster Wilson, Director of the East African Institute of Malaria and Vector-borne Diseases, for his helpful criticisms of this manuscript, and to the staff of the Pare Malaria Control Scheme for carrying out the routine catches described. We are also indebted to Mr. B. Weitz of the Lister Institute of Preventive Medicine, Elstree, England, for carrying out the precipitin tests, which formed an integral part of the experiment.

References.

- DRAPER, C. C. & SMITH, A. (1957). Malaria in the Pare area of N.E. Tanganyika. Part I. Epidemiology.—*Trans. R. Soc. trop. Med. Hyg.* **51** pp. 137-151. 47 11 0
- GILLIES, M. T. (1954). Studies of house leaving and outside resting of *Anopheles gambiae* Giles and *Anopheles funestus* Giles in East Africa. I. The outside resting population.—*Bull. ent. Res.* **45** pp. 361-373. 42 11 8

SMITH, A. & DRAPER, C. C. (1959). Malaria in the Taveta area of Kenya and Tanganyika. Part I. Epidemiology.—*E. Afr. med. J.* **36** pp. 99–113.

TRAPIDO, H. & AITKEN, T. H. G. (1953). Study of a residual population of *Anopheles l. labranchiae* Falleroni in the Geremeas Valley, Sardinia.—*Amer. J. trop. Med. Hyg.* **2** pp. 658–676.

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THE ERADICATION OF *GLOSSINA MORSITANS SUBMORSITANS* NEWST. AND *GLOSSINA TACHINOIDES* WESTW. IN PART OF A RIVER FLOOD PLAIN IN NORTHERN NIGERIA BY CHEMICAL MEANS. PART II.

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In a previous paper, MacLennan & Kirkby (1958) described the eradication, in 1956, of *Glossina morsitans submorsitans* Newst. from an isolated area of bush in Northern Nigeria by spraying the vegetation with a 5 per cent. aqueous suspension of DDT. That operation could be regarded as a pilot scheme for the development of a method to be applied to a more extensive area to the north-east, and subsequently elsewhere in the Sudan savannah zone of Northern Nigeria (Keay, 1949), which is an important cattle-raising area.

The conclusions drawn from the scheme were that since the tsetse concentrate in the thickets in the severe dry season, only those thickets need be treated, that the application of a 5 per cent. suspension of actual DDT to tree trunks will achieve eradication and that a single application only is sufficient.

The present paper describes the development of this technique and its application on a large operational scale in 1957 to an area infested with both *G. morsitans* * and *G. tachinoides* Westw.

The physical features of the country.

The operational area formed part of the flood plain of the river Komadugu Gana, also known as the Misau or Dingaiya, which flows northwards through Bulkachuwa in Bauchi Province to Dapehi in Bornu Province. To the south it was separated from the area dealt with in the previous paper by a natural barrier five miles in width at Bulkachuwa.

The plain varied in breadth from two to six miles and was bounded by either dry orchard woodland or farmland. The river occupied a bed about 30 yd. wide, strongly meandering and breaking off into numerous ox-bow lakes. In the rains the area became extensively flooded and the river overflowed into subsidiary channels, some of them large. These might hold water in parts through the dry season. In the year's operational area, which covered only 20 miles in a straight line, there were in the region of 100 miles of river and water course.

Vegetation.

MacLennan & Kirkby (1958) have listed the characteristic species of trees occurring south of Bulkachuwa, and their account applies equally to the present area. The general distribution of vegetational types is indicated in fig. 1.

(a) *The river bed.*

The river usually occupied a small channel within its bed during the dry season, leaving a shelf more or less thickly invested with *Syzygium guineense*, and *Mitragyna inermis* where the shelf was broad, as on the inside of a meander.

* Throughout this paper the subspecies *submorsitans* Newst. is implied when reference is made to *G. morsitans*.

(b) *The riverside thickets.*

The usual vegetation of the upper banks of the river was dense evergreen forest, often of true gallery type, which might extend 100 yd. or more from the bank. Characteristic species were *Khaya senegalensis*, *Ficus* spp., *Tamarindus indica*, *Celtis integrifolia*, and *Diospyros mespiliformis*, whose saplings often formed the underbrush. At the edges of the thicket were *Anogeissus leiocarpa*, *Dalbergia hostilis* and *Combretum* spp., usually heavily entangled with *Acacia ataxacantha*.

(c) *Subsidiary water courses and ox-bow lakes.*

When large, these might support thickets equal to those along the river itself, although they frequently showed signs of degeneration and contained a large proportion of dead wood. The bed of a water course was often completely occupied by dense *Syzygium* and *Mimosa pigra*, especially where there was permanent water.

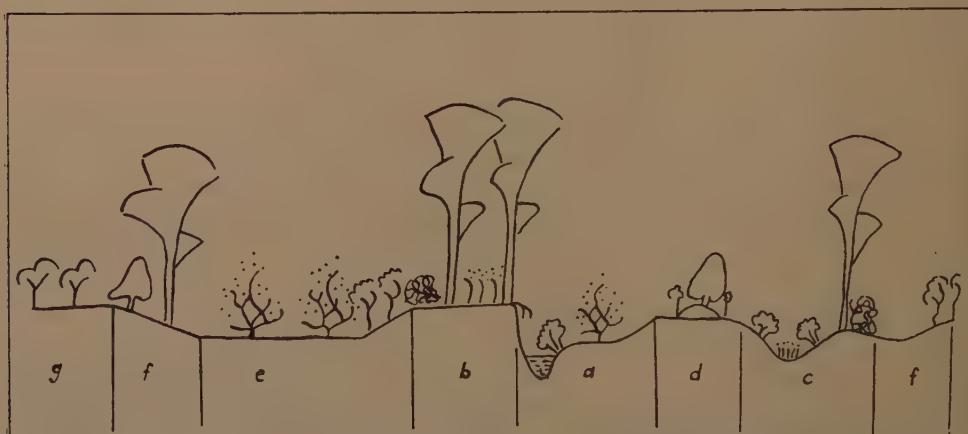


Fig. 1.—General distribution of vegetational types.

(d) *High open ground with clumps.*

About a third of the total area of land away from the river was of this type. The ground was hard and level, with sparse fine grass in the rains, and the clump character was given by the well-known and interesting association of vegetation with termite mounds. Typically, each termite mound carried one or more examples of *Tamarindus* or *Celtis*, several of *Balanites aegyptiaca*, and sometimes *Acacia ataxacantha*, such groups occurring 20 yd. or more apart.

(e) *'Fadama.'*

This local term conveniently describes the open tall grassland which is seasonally flooded and is bare of trees or has scattered *Mitragyna*. Where such an area met high ground the *Mitragyna* often grew thickly, with occasional pure stands of *Pseudocedrela Kotschyi*. There was a tendency for the water in draining off the fadama to form channels, sometimes closely lined with *Mitragyna*.

(f) *The edge of the upland.*

The flood plain was contained by a slight rise, often barely perceptible, between fadama and orchard bush. This narrow slope frequently bore a distinctive type

of vegetation which has been referred to as 'ecotone'; typically the most conspicuous species were *Khaya*, *Ficus* spp. and *Tamarindus*, the last forming occasional clumps, as in (d), sometimes as far as half a mile into the upland. At the extreme lower edge of this zone *Pseudocedrela* was abundant.

(g) *The upland.*

Mainly comprising *Combretum* spp., *Acacia* spp., *Terminalia* spp., *Piliostigma* spp. and *Anogeissus*, this open orchard bush did not support *G. morsitans* in the dry season and therefore effectively limited the area of work. In many places cultivation had advanced to the extreme edge of the flood plain.

Climate.

Nash (1937) has described very fully the climate over almost three years at Gadau, some 40 miles east of the present area. Gadau appears to be somewhat the drier of the two.

During the present season's work a continuous record was made of temperature and humidity in a Stevenson screen by means of a thermohygrograph consisting of a bimetal strip thermometer and a hair-type hygrometer. The latter was later found to be badly out of adjustment and its record had to be discarded.

Thicket temperatures at ground level averaged 7°F. less than temperatures at 5 ft. in January, 5.5°F. less in February, 5°F. in March and 5°F. until 26th April when the taking of thicket temperatures was abandoned.

The general pattern of the dry season may be summarised as follows. Rain ceased in October, but the area was waterlogged in parts until mid-December. By mid-February the drying up, defoliation and burning were advanced enough to make the contraction of tsetse distribution evident. At the end of March the weather became unsettled; the first shower fell on 29th April and on 14th May the true rains began.

Game.

Compared with the food supply of *G. morsitans* in some other parts of its range, that available here must be considered poor, and doubtless this fact contributed to the tsetse's susceptibility to adverse climatic influences.

The most abundant mammal was the warthog, which laid up during the day, generally in the thickets. Other mammals present included crowned duiker, roan antelope, hartebeest, bushbuck, oribi, reedbuck, species of gazelle, porcupine, cane-rat and two species of monkey. Buffalo were believed to visit the area occasionally in the rains, and a lion spoor was once seen. Crocodiles occurred sparingly, mainly in the ox-bow lakes.

Distribution of tsetse.

G. morsitans was the more numerous of the two species present. An adequate working knowledge of its distribution within its broad habitat had been gained by simple observation rather than by detailed statistical examination; the comparative inaccessibility of the area in the rains made any planned scientific investigation very difficult.

During the rains, the fly were fairly generally distributed through the area and penetrated some distance into the upland to the west. From December onward, as the weather became more severe, progressive concentration occurred into such situations as afforded a more suitable microclimate; the denser patches at the edges of the upland, the larger termite-mound clumps, and above all, the thickets. Maximum concentration was reached in March and April, and dispersal began again at the end of May.

The principal breeding sites were of necessity in the thickets throughout the year. No breeding was found in the termite-mound clumps.

G. tachinoides, being more or less dependent on the proximity of water, had a more restricted habitat in the area. It occurred on the river banks, throughout, under the *Syzygium* and in the thickets; in the subsidiary channels and ox-bow

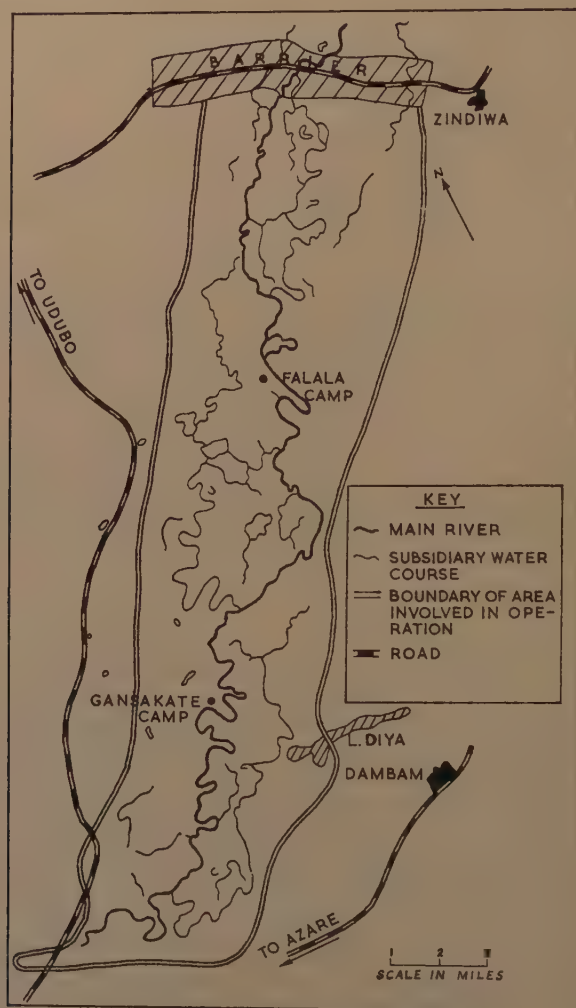


Fig. 2.—Map showing eradication area, 1957.

lakes it was associated especially with *Mimosa*, and was by no means invariably absent when the channel was dry. There was probably little seasonal change in its distribution.

The application of the insecticide.

The preparation of the area.

The area infested by *G. morsitans* and *G. tachinoides* was continuous from Bulkachuwa to near Dapchi, a distance in a straight line of about 90 miles.

It was therefore considered necessary to isolate the portion chosen for the year's work by means of an artificial barrier. After aerial survey a suitable site was chosen, rather more than 20 miles from Bulkachuwa, and ruthless clearing was carried out here, over a zone six miles wide by one mile deep, at the same time as spraying began at the southern end of the infested area. The part of the infested area thus isolated was approximately 80 square miles.

As soon as the ground on the flood plain was dry enough to carry vehicles in December, a camp was established at Gansakate (see fig. 2), and roads were cleared through the bush following both banks of the river and all other channels. Where a large area of clumps existed, a road was made across it.

At the same time, footpaths were cut into the thickets and denser clumps to allow free access by the operators to all parts. Any large patches of *Mimosa* were traversed by intersecting paths cut at intervals.

An important part of the preparation was considered to be the achieving of as fierce and complete a grass-burn as possible. This would not only improve the penetration of the hot dry 'Harmattan' wind into the thickets, but also promote a heavy leaf fall especially in the *Mitragyna*. It was, moreover, of great practical value in assisting movement and visibility in the bush.

Spraying.

As in the work of 1956, DDT 50 per cent. dispersible powder was used in aqueous suspension at a concentration of 5 per cent. DDT. Spraying was confined to the waterside *Syzygium* and *Mimosa*, the thickets, the denser clumps, isolated *Mitragyna* which provided shade, and larger trees in the upland fringes. Any situation exposed to the sun or to the desiccating effect of the wind was ignored. Except in the case of *Mimosa*, only trunks of diameter greater than about 6 in. were sprayed, up to a height of about 5 ft. above ground-level. *Mimosa* patches were sprayed only at the edges of the cut paths. No creepers, twigs or leaves received any intentional deposit. Special attention was paid to holes and crevices, low overhanging limbs, fallen trees and overhanging roots in the river banks. Large animal burrows were well sprayed inside. As climatic conditions became more severe and defoliation progressed, the number of sites requiring spraying decreased. Refoliation in some species of tree occurred after the end of March.

The quantity of insecticide applied was such that the bark of the tree was thoroughly soaked, but that fluid did not run down. Operators were trained to use regular economical movements of the spray lance, but close regulation of spraying technique such as is achieved in mosquito control was not possible under these conditions. A correct application showed, on drying, as a conspicuous whitish deposit (a very significant advantage for checking purposes). Seven samples showed an average deposit of 111 mg. per sq. ft. (range 58-234 mg. per sq. ft.).

Equipment and staff.

Two types of pneumatic knapsack sprayers were used; twenty-six Four Oaks Kent hand-charged models and eight motor-charged Favori. The latter, not being as mobile as the hand-charged sprayers, were used mainly in the heavier riverside thickets that were well served with roads. The DDT suspension was prepared in quantities of 40 gallons using the steel drums in which the DDT was supplied, and was transported from the mixing site to the sprayers in 4-gal. kerosene tins.

One 5-ton and two 2-ton lorries, and two long wheel-based Land-Rovers were used for the transport of personnel, equipment and materials; late in the season two tractors and trailers were acquired.

Five European officers were present; the two authors supervised spraying, one officer the preparatory phases, and two the cutting of the barrier. Fifteen trained Nigerian junior staff assisted in the supervision of up to 150 labourers locally recruited for spraying, road making and path cutting, while up to 500 labourers were employed in clearing work at the barrier.

Timing.

The period during which work could be done was limited in two senses; there were the physical limits of access to the area, and the practical limits imposed

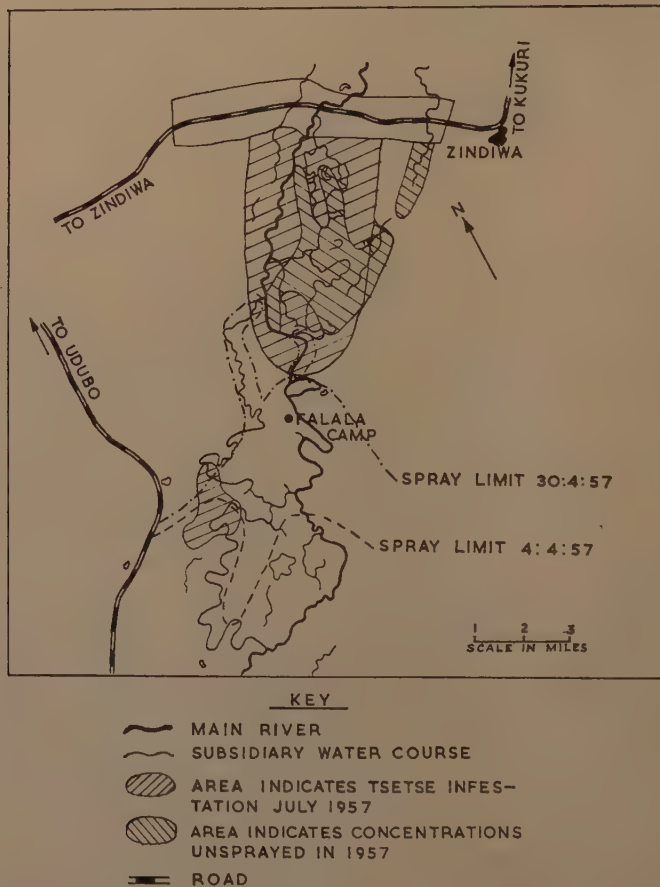


Fig. 3.—Map showing spray limits, 1957.

by the change of season upon the effectiveness of the spray. Thus it was found impossible to enter the area for preparatory work before December, and motor transport had to be withdrawn at the end of May. Within this period, the concentration of tsetse was considered far enough advanced for spraying to begin by the middle of February, and it will be suggested below that spraying after the end of April was ineffective. The total number of days worked in the spraying operation was 73.

Results.

The siting of the barrier proved to have been based on an optimistic estimate of the rate of working and the length of the spraying season. By the end of April it became obvious that the area would not be finished before the rains, and during the remaining time an effort was made to attack the surviving tsetse by spraying the major foci only. It was hoped thus to reduce the population pressure on the borders of the fully treated portion. When the team was withdrawn on 21st May, the extent of the treated areas was as shown in fig. 3.

A small survey party maintained a constant watch on the treated areas through the season. Its main function was to detect failure of control at any spot where it might occur, but a few random catches in recently sprayed places indicated the decline of the population towards extinction (Table I). Following the discovery of any unsprayed areas, a small mobile team of 2-4 operators was sent to spray them.

TABLE I.

Decline in the tsetse population after spraying. Numbers of flies taken in random catches.

Weeks after application	Average catch per patrol	Percentage teneral flies	Remarks
Sprayed in February :			
4	7.5	60	{ Adjacent to an unsprayed area
5	1.0	100	
5	11.0	2	
7	0	—	
8	0	—	
Sprayed in March :			
1	2	75	
2	4	25	
3	2.7	63	
4	0.8	75	
5	0	—	
6	0.4	66	
7	0	—	
8	0	—	
Sprayed in April :			
2	0.5	—	
3	3.0	33	
4	0	—	

It was to be expected that, after the rains had begun, newly emerged tsetse would encounter conditions favouring their dispersal from the thickets, and even within the thickets much of the insecticide would be washed away. The insecticidal treatment was thus likely to be only partially effective when applied at an interval before the rains of the maximum pupal period (under existing conditions) or less.

This expectation proved to be true. A thicket sprayed on 9th May was examined four weeks later, and the catch of *G. morsitans* obtained was shown to consist predominantly of young specimens. Of the 40 flies caught here and 78 caught in an unsprayed thicket, 22.5 and 2.32 per cent., respectively, were teneral. To avoid inaccuracy arising from any errors by the Control Assistants in determining teneral flies, the whole of each catch was examined for wing fray,

TABLE II.
Costs other than capital.

	Roads	Thickets	Fly-rounds	Spray operators	Transport drivers	Camps	Barrier	Cost of insecticide : Cost of application : Labour Petrol Total Barrier Grand Total
Nov.	65. 5. 9	—	54.15. 0	—	11. 9. 8	15.14. 7	—	£2,000. 0. 0
Dec.	127.13. 5	6. 9. 2	44.10. 8	—	17. 8.10	38. 4. 6	—	
Jan.	151. 6. 6	49. 3. 0	47. 5. 2	—	19. 2. 2	7.10. 1	—	
Feb.	260.16. 2	139.10. 0	33.12. 0	49. 9. 1	40.14. 3	63. 0. 0	—	£3,140. 4.11
Mar.	167.18. 3	123.16. 1	47.17. 6	108.17. 6	52.13. 0	26. 0.10	3,022. 1. 7	£ 250. 0. 0
April	203.14. 6	139. 8. 0	51. 7.10	353. 0.10	45.18. 0	62.12. 9	1,566. 6. 4	£5,390. 4.11
May	100. 5. 1	147. 8. 1	44.16. 0	216. 4. 7	5. 6. 1	—	1,499.19.10	£6,088. 7. 9
	£1,076.19. 8	£605.14. 4	£324. 4. 2	£727.12. 0	£192.12. 0	£213. 2. 9	£6,088. 7. 9	£11,478.12. 8

using Jackson's standards (1946) applied to each wing independently. The percentages assigned to each fray stage are shown in fig. 4.

Surveys carried out after the end of the spraying operation showed fly still present in all that part of the area sprayed after the end of April.

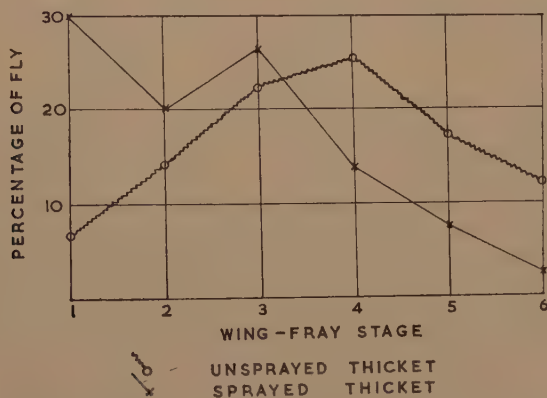


Fig. 4.—Distribution of wing-fray stage in two samples of *G. morsitans*.

Costs.

Costs are set out in Table II. It is immediately apparent that the cost of the barrier at £6,088 or about £1,000 per square mile was disproportionately high when compared with the cost of £5,390* for the eradication of *G. morsitans* in an effective area of 55 sq. miles, or about £98 per sq. mile. If capital depreciation on vehicles and equipment, estimated at £1,000, is included, the cost becomes £116 per square mile.

The general labour rate during the scheme was between 2s. 4d. and 2s. 8d. per man/day. Salaries of departmental officers were not included as it was difficult to fix a fair figure; their work lay elsewhere at other times of the year. It should be borne in mind that *G. tachinoides* was also eradicated.

Discussion.

The present scheme has demonstrated that eradication of *G. morsitans* and *G. tachinoides* in this habitat and under these conditions is possible by a single selective application of DDT. As is usual in an operation of this type, the emphasis is on obtaining immediate and certain results; with later opportunities for experiment it is likely that considerable refinement of the technique will be achieved.

In practice there was a strong personal element present in the spraying process. The two officers were in constant close direct control of the operators, and considerable subjective judgment was used in the selective application of the DDT. In order to cover the whole area efficiently it was desirable to have large-scale maps of the river system; since none were available and since even the existing small-scale maps were highly inaccurate, tracings were made from aerial photographs to a scale of $2\frac{1}{4}$ in. to the mile. It was necessary to become familiar with every

* This figure, which is shown in Table II, includes the value and cost of application of insecticide used in May, beyond the 55 sq. miles, although, as mentioned above, this treatment was found to have been ineffective.

detail of the topography, and to exercise ingenuity in directing movements so as to deal with every part reliably and economically; the broken nature of the country made any simple geometrical movements impossible. It is hoped later to embody the technique evolved in a set of easily applied rules, but the need for some personal control and judgment will never be entirely eliminated.

The possible improvements in technique which are envisaged are as follows:—

1. Reduction of the concentration of DDT used.
2. Increased selectivity of application.
3. Extension of the season (only possible by beginning earlier); depending on the persistence obtained, it should be possible to apply the DDT before the time of concentration of the tsetse.

It seems evident that these three considerations are in mutual opposition and that the ideal will prove to be a compromise, perhaps varying through the season.

Although it is unfortunate that the work was not completed as far as the barrier, it is to be hoped that something will be learnt from the situation. The long, narrow shape of the area under treatment and its isolation from other tsetse-infested areas are factors which tend to simplify the task of eradication. Whether or not a physical barrier will in future be needed at the limit of each year's work depends upon the extent of re-invasion to be expected and the cost of re-spraying the invaded country. In the present instance, subsequent observation (Davies & Blasdale, 1960) has shown that, by the end of January 1958, re-invasion of the northern part of the sprayed area had penetrated to a distance of only a little over two miles. The area effectively cleared of fly was, therefore, 48 sq. miles.

Summary.

A stretch of river with its flood plain, a habitat of *Glossina morsitans submorsitans* Newst. and *G. tachinoides* Westw. in the Sudan savannah zone of Northern Nigeria, which is an important cattle-raising area, is described.

An effective technique for the eradication of both species of tsetse has been developed, using a single application of a 5 per cent. aqueous suspension of DDT by knapsack sprayer in the places of dry-season concentration of the fly, and on the principal midday resting sites, viz., between ground-level and a height of 5 ft. on tree trunks greater than 6 in. in diameter.

The area was accessible between November and May, but fly distribution was considered appropriate for spraying only between February and April. Re-invasion by the fly into parts of the area from which it had been eradicated was expected, but the narrow shape of the area made it possible to cut a barrier of ruthless clearing a mile in width and extending from edge to edge of the flood plain. Spraying operations did not in fact reach the barrier, but re-invasion from the unsprayed part was nevertheless found subsequently to be on a small scale.

The clearing of the ruthless barrier cost about £1,000 per sq. mile, whereas the eradication of the fly cost about £98 per sq. mile, over an effective area of 55 sq. miles: of this, 48 sq. miles remained free of fly by the following dry season. It may therefore be cheaper to tolerate re-invasion, between one operational season and the next, than to prevent it.

Acknowledgements.

The authors acknowledge their debt to Mr. K. J. R. MacLennan, M.B.E., head of the Tsetse Control Unit during the period of the operation described; and to Dr. S. G. Wilson, C.B.E., then Director of Veterinary Services, on whose suggestion this account was written.

Mr. W. I. A. Dees, Senior Control Officer, played an important part in the initial stages of the work, and all Senior and Junior staff deserve mention for their intensive efforts under hard conditions.

Help given by the Sleeping Sickness Service, Ministry of Health, in providing mechanical saws and skilled labour in clearing a section of the barrier is gratefully acknowledged.

References.

- DAVIES, H. & BLASDALE, P. (1960). The eradication of *Glossina morsitans submorsitans* Newst. and *Glossina tachinoides* Westw. in part of a river flood plain in Northern Nigeria by chemical means. Part III.—*Bull. ent. Res.* **51** pp. 265–270. newcl
papers
- JACKSON, C. H. N. (1946). An artificially isolated generation of tsetse flies (Diptera).—*Bull. ent. Res.* **37** pp. 291–299. 34 199
- KEAY, R. W. J. (1949). An outline of Nigerian vegetation.—52 pp. Lagos, Govt. Print. — —
- MACLENNAN, K. J. R. & KIRKBY, W. W. (1958). The eradication of *Glossina morsitans submorsitans* Newst. in part of a river flood plain in Northern Nigeria by chemical means.—*Bull. ent. Res.* **49** pp. 123–131. 46 7
- NASH, T. A. M. (1937). Climate, the vital factor in the ecology of *Glossina*.—*Bull. ent. Res.* **28** pp. 75–127.

APPENDIX.

Persistence of DDT under field conditions.

A thicket to the south of Bulkachuwa was sprayed in August 1955 with 5 per cent. actual DDT and tests for persistence were made by placing 10 individuals of *G. morsitans* in a Bruce box with sprayed bark. Up to eight weeks after spraying, flies in contact with treated bark were dead after three hours' exposure, whereas controls were alive at 24 hours.

This test was rather artificial in that in a cage more parts of a tsetse's body than the tarsi are likely to come into contact with the DDT; this would be likely to produce a favourable result, and therefore an alternative test was done in January and February 1957. In this case the tarsi only of the flies were allowed to come into contact for 10 seconds with a piece of sprayed bark, and the flies were then placed in tubes. Control flies were exposed on unsprayed bark and also placed in tubes. Alternate pairs of tsetse were used for test and control. A small piece of water-damped filter paper was placed in each tube, as the prevailing humidity was very low.

In September, at the end of the rainy season, further tests were carried out, the only difference being that the flies caught were randomised into 'test' and 'control' cages and that the flies were fed for 10 minutes after exposure to the insecticide, at least half usually engorging.

The results shown in Table III indicate that samples of bark taken four months after the spraying of DDT appeared to show significant toxicity, though the six-month-old samples were apparently not toxic at all. However, continuous exposure of flies to these samples in cages showed, in one case, some toxic effect at eight hours, though little at five hours; another gave 100 per cent. mortality in 19 hours. A four-month-old sample produced 100 per cent. mortality after two hours of continuous exposure.

In trying to relate these tests to what happens during reclamation, it must be remembered that insecticide is applied to all the concentration habitats that can be found, and that probably means most of them. Therefore, on favoured resting sites in the concentration habitat, it is probable that an exposure longer than 10 seconds occurs during the life of the tsetse. It seems reasonable to suppose that a fall in persistence as indicated by a 10-second exposure test read at 4-5 hours does not necessarily mean that control can no longer be expected. The limit of useful persistence is not yet known, but is at least 52 days on bark.

TABLE III.

Persistence of DDT on bark as shown by mortality in tsetse flies the tarsi of which had been in contact with the treated surface for 10 seconds.

Days after application	Mortality (%) after 10 seconds' exposure		
	Test	Control	Adjusted kill
26	83	12	81
32	92	33	88
38	65	27	52
52	36	7	31
120	23	0	23
180 (Sept.)	25	33	0

The duration of effective persistence is of great practical importance, as the times of adequate concentration of the tsetse are limited and uncertain. The only means of extending the spraying season is to begin before concentration is complete, but the limitation on this is the unknown persistence period of the insecticide.

THE ERADICATION OF *GLOSSINA MORSITANS SUBMORSITANS* NEWST. AND *GLOSSINA TACHINOIDES* WESTW. IN PART OF A RIVER FLOOD PLAIN IN NORTHERN NIGERIA BY CHEMICAL MEANS. PART III.

By H. DAVIES and P. BLASDALE

26.

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The Komadugu Gana (Misau) river flows, for part of its length, in a north-easterly direction through the Sudan savannah vegetation zone of Northern Nigeria (Keay, 1949), which is an important cattle-raising area. *Glossina morsitans submorsitans* Newst. infests the flood plain and adjacent uplands of this river from a point near Akwiam in the south (see fig. 1) for a distance of approximately 120 miles to the north-east. This fly-belt extends, in places, to almost 10 miles in width and is isolated.

G. tachinoides Westw. also infests this area but is also found south of Akwiam, although its northernmost limit is only a few miles north of the boundary of the infestation of *G. morsitans*.*

Successful measures adopted in 1956 to eradicate *G. morsitans* from the southern portion of this area, between Akwiam and Bulkachuwa, by spraying of vegetation with DDT have been described by MacLennan & Kirkby (1958). Continuation northwards of this work during the dry season of 1957 has been described by Kirkby & Blasdale (1960).

The present paper refers to a further extension of this work carried out during 1958, and draws special attention to the lessons learnt, modifications of technique evolved and methods now adopted in the eradication of both *G. morsitans* and *G. tachinoides*. Although reference is only made here to reclamation carried out up to the end of the 1958 season, work is continuing annually until the whole infestation, north of Akwiam, is eradicated.

Previous history.

The areas reclaimed during 1956 and 1957 are shown in fig. 1. Details of climate, vegetation and certain ecological factors concerning the tsetse fly in this area have been described by the authors mentioned above.

Work during 1956 was directed mainly towards the elimination of *G. morsitans* by means of a DDT spray in an area, 7 square miles in extent, that was isolated from the main focus by a natural barrier at Bulkachuwa, and this was a complete success. Work during 1957 was intended to eradicate both *G. morsitans* and *G. tachinoides* from the area between the natural barrier at Bulkachuwa and an artificial ruthless barrier that was cleared between Bulaudo and Zindiwa, rather more than 20 miles to the north (fig. 2). It was found to be impossible to complete the application of insecticide up to this barrier by the end of the 1957 spraying season, before the start of the rains. This barrier had, therefore, no effect in preventing the re-invasion of the southern, sprayed, part by tsetse from the northern, unsprayed, part during the wet season of 1957.

* Throughout this paper the subspecies *submorsitans* Newst. is implied when reference is made to *G. morsitans*.

Re-invasion by tsetse of the zone sprayed in 1957.

It was found, during the wet season of 1957, that, apart from re-invasion in the north, scattered flies of both species existed in the sprayed area, mainly single specimens caught in widely separated places. It was thought that these were stray flies and that the density in which they were found could not support a permanent population. This surmise proved to be correct and further examination during the following dry season failed to reveal a single fly in such places.

A thorough survey, carried out immediately before the 1958 season's task was begun, to ascertain to what extent the main body of fly had re-invaded the

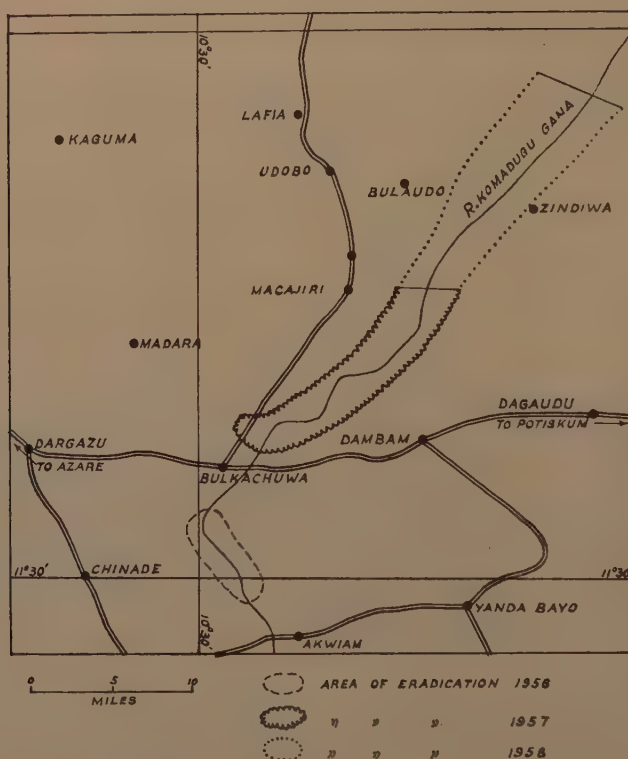


Fig. 1.—Progress of tsetse eradication in the Komadugu Gana flood plain, 1956–1958.

northern portion of the sprayed area, indicated that the front had penetrated only to a distance of a little over two miles. The 1958 season's work was therefore started about one mile south of this front (see fig. 2).

Application of insecticide.

The insecticide used was, as in previous years, 50 per cent. DDT wettable powder in aqueous suspension at a strength of 5 per cent. DDT. Half-way through the season a weaker suspension of 3.75 per cent. was used. This latter strength proved to be adequate for complete eradication.

Application was carried out by means of the same two types of knapsack sprayers as those used during the previous season, *i.e.*, the Colibri and the Four

Oaks Kent. The same 28 Four Oaks sprayers were employed but the Colibri units were increased in number to 23 and equipped with hand-charging attachments. Thus, both models had the advantage of being able to function in bush well away from tracks and were supplied by carriers. The Colibri sprayers, when used in areas adjacent to motor tracks, could still be filled by an engine-operated machine and this greatly increased the speed of operation.

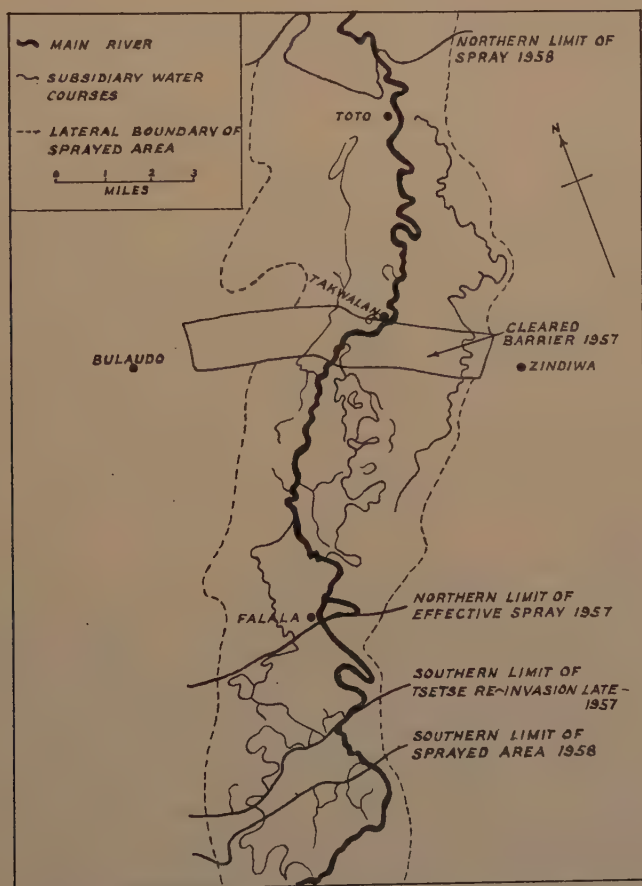


Fig. 2.—Detail of area sprayed in the vicinity of the Komadugu Gana river, 1958.

It had been found previously that during the morning and evening, when flies could be caught out in the open off bushes, leaves, ground and bait, a typical sex ratio indicating a concentration area of *G. morsitans* was apparent, namely, an extremely high proportion of males. However, during the hottest part of the day the majority of the fly population was found to be resting on the larger tree trunks, in shade, up to a height of about 5 ft. Catches here, made at this time, contained a high percentage of females.

It was therefore decided to confine spraying, even more than in previous years, to the trunks of trees exceeding about eight inches in diameter and well shaded by their canopies or adjacent thicket. No spraying was done above a height of

about 5 ft. Leaves, twigs and branches of the trees and of the surrounding shady shrubs were ignored. Care was taken to spray all sides of the trunk. The insecticide was applied with steady sweeps of the lance and application ceased before the white liquid was seen to run down the bark. This method of spraying is fairly straightforward and has the great advantage that illiterate operators can be easily and quickly taught what vegetation requires spraying and what should be missed. Borderline cases are, however, frequent, especially where large trees not enveloped by much thicket are encountered. Therefore constant supervision, even of the more experienced operator, is necessary.

It was necessary to have gangs of labourers preceding the pumps and cutting paths through the thickets and forest islands up to and around each large tree. This may create the impression of a formidable task, but it was surprising how few paths were necessary in each forest island to enable access to be gained to each tree. Very often a large clump thicket was centred around one main tree, usually of the species *Tamarindus indica* or *Celtis integrifolia*, and only this single tree was sprayed.

When dealing with riverine vegetation, where the low-flying *G. tachinoides* was prevalent as well as *G. morsitans*, the tree trunks of smaller diameter were also sprayed. Where shrubs such as *Mimosa pigra* were very thick and low-lying, intersecting paths were cut and the sides of the paths sprayed.

Road construction was started as soon as possible after the 1957 wet season but occupation of the first camp, Falala, could not take place until the end of November. The first spraying took place at the end of January and operations continued until the end of April, by which time the area treated extended well north of the cleared barrier. As in previous years, actual application of insecticide was limited to the dry-season period.

All labour and staff lived in temporary camps which were moved forward as progress was made.

Success of eradication.

Surveys carried out 18 months later (at the end of 1959) of the area reclaimed during 1958 have failed to detect a single tsetse fly. This indicates that the season's reclamation was a success and that the northward extension of the eradication work during the subsequent season has prevented any re-invasion from that direction. Before spraying, infestation by *G. morsitans* in the area was heavy, and most of the fly-rounds provided a catch of over 35 flies per mile patrolled. The density of *G. tachinoides* exceeded ten flies per boy-hour on many of the more favourable stretches of river.

The area sprayed in 1956 was still clear of *G. morsitans*, but *G. tachinoides* was found two years later due to re-invasion from the south, in which direction the distribution of this species had been continuous with the area sprayed (MacLennan & Kirkby, 1958). This has now been rectified by isolating this area from the south as a result of the clearing by the Ministry of Health, of a ruthless barrier in the vicinity of Akwiam and respraying the riverine vegetation.

The area sprayed in 1957 was still free from both species.

Cost and administration.

Since many of the staff employed and much of the transport used on the scheme were engaged on other work at different times of the year, it is only possible to calculate, with any degree of accuracy, the value of insecticide used and cost of labour employed.

The total area sprayed during the current season amounted to 69 sq. miles. The quantity of insecticide used was 31,500 lb. of DDT 50 per cent. wettable powder, averaging nearly 460 lb. per sq. mile. The price in Nigeria was £2,800. Labour costs during the period added up to £3,160. Therefore the cost of

reclaiming the area, in so far as material and labour are concerned, amounted to approximately £86 per sq. mile.

Although capital costs and depreciation are not included it should also be realised that the area of grazing land made safe for cattle was much larger than the actual area sprayed, since, during the wet season, *G. morsitans* in Northern Nigeria is by no means strictly confined to the recognised limits of the fly-belts.

Administration of a scheme of this kind is complicated. Success depends on adequate supervision of labour, ahead of the main effort, to provide tracks for transport and paths for spray operators, strict control of the spray teams and constant checking of the sprayed area: pockets of flies missed, and not discovered in time, might possibly nullify the season's work and also jeopardise previous reclamation work in this fly-belt.

Discussion.

Nearly all schemes designed to eradicate tsetse flies by insecticides have relied on successive applications of the chemical to vegetation in the infested zone; the length of pupal period may mean that young flies emerge up to six weeks or more, according to climatic conditions, after the first application, and therefore, unless the residual lethal effect is adequate, a second and often a third application is necessary. During the first year's operations on the Komadugu Gana river, two applications were made to most of the area, but during the second and third years the ground was covered only once and this was found to be sufficient.

The fact that the insecticide is applied during the dry season is an important factor contributing to its success.

If all shady spots or all parts of the vegetation on which flies are likely to rest had to be sprayed, the scheme would not be economical; too little ground would be covered in one season and costs would be prohibitive. The discovery that application of insecticide to the lower part of the larger tree trunks, in shade, is sufficient to eradicate *G. morsitans* in this area, is an important one.

Breeding was often heavy between the buttresses of trees, and insecticide dropping on the ground adjacent to the tree trunk may have had some effect on newly emerged flies, but as large numbers of breeding places scattered in shade under thickets in forest islands were not touched, it is fairly safe to surmise that it was chiefly the effect, on adults, of the insecticide applied to tree trunks, that caused complete eradication.

During the first year's work in this fly-belt the existence of a natural barrier to protect the sprayed area from the rest of the belt was considered to be essential to the success of the scheme (see fig. 1). During the second year, when no natural barrier existed, a costly artificial barrier was cleared in order to protect the season's work. As the spray teams failed to reach it before the end of the dry season, the barrier was useless for the purpose for which it was created. At the start of the third year's work it was found that the fly had only re-invaded the area sprayed in 1957 to a depth of about two miles, and it is therefore considered that, in a comparatively narrow and elongated fly-belt of this kind, the clearing of a barrier is not necessary. The ground lost to the fly can easily be recovered by respraying in the following season. This is more economical than cutting down bush to form a barrier.

G. morsitans is a more dangerous fly than *G. tachinoides* where livestock is concerned and is a much more difficult fly to eradicate. It is the technique evolved in eliminating the savannah species, *G. morsitans*, that is the most important feature of this project.

Efforts are still continuing to find out whether spraying can be even more selective, but events described above indicate that a technique has been evolved that will, in time, free the Sudan savannah vegetational zone from infestation by tsetse flies.

Summary.

An account is given of work carried out during the third year to eradicate *Glossina morsitans submorsitans* Newst. and *G. tachinoides* Westw. from an elongated fly-belt situated in the Sudan savannah vegetational zone of Northern Nigeria, which is an important cattle-raising area.

The total area of the fly-belt, which is isolated as far as *G. morsitans* is concerned, measures about 120 miles in length and extends, in places, up to almost 10 miles in width. The country involved forms the flood plains and adjacent uplands of the Komadugu Gana river.

Sixty-nine sq. miles were sprayed with DDT during the 1957-58 dry season (between end of January and end of April 1958), and 18 months after completion of work no tsetse has been found in the treated area. These 69 sq. miles formed the dry-season habitat of the fly on this section of the river, and the cost of insecticide and labour involved amounted to approximately £86 per sq. mile. As the zone infested in the wet season greatly exceeded this dry-season concentration area, reclamation costs per sq. mile, when applied to the amount of grazing land made safe for cattle, amounted to much less than the figure quoted.

Successful continuation of this project is ascribed to three salient features of the technique employed:—

- (a) A single application only, of a 3.75 per cent. aqueous suspension of DDT from a wettable powder, is sufficient for complete eradication.
- (b) A high degree of discriminative or selective spraying is possible: for the elimination of *G. morsitans*, spraying can be mostly confined to larger tree trunks, in shade, up to a height of about 5 ft.
- (c) Artificial or natural barriers to isolate each season's work, and so prevent re-invasion, are not necessary where the fly-belt is of a comparatively narrow and elongated nature. Spraying the re-infested area during the following season is more economical.

Acknowledgements.

Acknowledgements are due to Mr. W. W. Kirkby, M.B.E., Principal Veterinary Officer, who was closely associated with this work, and to Dr. S. G. Wilson, C.B.E., Chief of Veterinary Research Division, for advice and encouragement and under whose direction the Scheme was carried out.

References.

- KEAY, R. W. J. (1949). An outline of Nigerian vegetation.—52 pp. Lagos, Govt. Print.
- KIRKBY, W. W. & BLASDALE, P. (1960). The eradication of *Glossina morsitans submorsitans* Newst. and *Glossina tachinoides* Westw. in part of a river flood plain in Northern Nigeria by chemical means. Part II.—*Bull. ent. Res.* **51** pp. 253-264.
- MACLENNAN, K. J. R. & KIRKBY, W. W. (1958). The eradication of *Glossina morsitans submorsitans* Newst. in part of a river flood plain in Northern Nigeria by chemical means.—*Bull. ent. Res.* **49** pp. 123-131.

THE NATURAL ENEMIES OF THE LETTUCE ROOT APHID, *PEMPHIGUS BURSARIUS* (L.).

By J. A. DUNN

E.M.N.

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Pemphigus bursarius (L.) overwinters in the egg stage on poplar (*Populus*) and, on hatching in spring, the fundatrices cause the formation of hollow, flask-shaped galls on the leaf petioles. They become enclosed in these galls where they mature and reproduce. Their progeny also develop within the galls and when the first of these fundatrigeniae are mature, the galls open to allow them to migrate to lettuce and other secondary hosts. The roots of these plants become colonised by the aphid, which remains underground until autumn when migration back to poplar occurs. Thus throughout most of the spring and summer the habitats of *P. bursarius* and, as a result, the associated natural-enemy complex, differ considerably from those of foliage-feeding aphids. Little work has been done on the natural enemies of gall-living and subterranean aphids, and it is hoped that the following information, which was obtained when studying the biology of *P. bursarius*, will help to stimulate more research into the subject.

Parasites.

In contrast to the foliage-feeding aphids, *P. bursarius* is relatively unaffected by parasites. This may be because its habitats and waxy secretions render it inaccessible to the majority of primary parasites of aphids which, with their long antennae and wings, are particularly vulnerable to mechanical injury.

During the present work, only the fundatrices of *P. bursarius* have been found parasitised and only adults of the Pteromalid, *Pachyneuron* sp., have emerged from these. It is assumed that, like other members of the genus, this species of *Pachyneuron* is hyperparasitic. No record of any parasites of *Pemphigus bursarius* could be found in the literature.

During the years 1955 to 1958, the incidence of parasitism in the Wellesbourne area was low although, at one site on 13th July 1956, more than 25 per cent. of the galls of *P. bursarius* on Lombardy poplar (*Populus italica*) contained parasitised fundatrices, most of which failed to yield any adult parasites, *Pachyneuron* sp. emerging from the remainder.

Predators.

It is proposed to deal with the predators of *P. bursarius* in the order in which they affect successive stages of the life-cycle.

Predators at the pre- and post-gall formation stages on poplar.

In early spring whilst a newly hatched fundatrix is seeking out and establishing itself on a leaf stalk it may be attacked by predators such as ladybirds. However, its small size and the way in which it often secretes itself under bud scales whilst it initiates a gall, operate against potential predators.

Once enclosed within a gall the aphid is usually safe from insect predators until the mouth of the gall opens at migration time, about three months later. Occasionally, however, galls become damaged by caterpillars such as those of the winter moth (*Operophtera brumata* (L.)) and the contents can then be attacked

by predators which normally would have to wait for mature galls to open. Predators can also gain early access to galls that close imperfectly.

Birds.

Birds often open up and eat the contents of maturing galls. In one row of 50 Lombardy poplars near Stratford-on-Avon, greenfinches (*Chloris chloris*) were observed going so methodically from gall to gall that later few galls could be located undamaged and with their aphid contents present. Similarly, almost all the galls in a group of these poplars at Welford-on-Avon were found to have been opened by birds, which circumstantially were thought to have been bluetits (*Parus caeruleus*).

Syrphids.

A small Syrphid larva can enter a gall which has opened and find without further search a supply of aphids which is probably adequate to meet all of its food requirements for larval development. Roberti (1938) inferred that this often happened in Italy but did not say what species of Syrphids were involved. Börner & Heinze (1957) listed no Syrphids as predators of *P. bursarius* but recorded the Syrphids, *Pipiza festiva* Mg. and *Phalangus virens* (F.), as predators of *Pemphigus spirothecae* Pass., an allied species which also produces galls on poplar.

During the present work, Syrphid larvae of the genus *Pipiza* have been found feeding on *Pemphigus bursarius* within the galls, but all larvae died before pupating and their specific identity remains unknown. Heiss (1938) stated that all known species of *Pipiza* were aphidophagous and that they preferred aphids with waxy secretions. She mentioned how well protected and difficult to see they were when "buried among waxy masses of their host and dusted with the same material." This was true of *Pipiza* larvae found in galls of *Pemphigus bursarius* and without special care it was easy to overlook them. They were not common and their distribution tended to be patchy and sometimes limited to a few galls in close proximity to each other. This was probably the result of very localised activity by egg-laying females. However, in mid-July 1956, 20 per cent. of the galls of *P. bursarius* on poplar at one site near Wellesbourne contained larvae of *Pipiza* spp. At this site, *Pipiza* larvae were also found in the galls of *Pemphigus protospirae* Licht., *P. filaginis* (Boy.) and *Thecabius affinis* (Kalt.). The larvae of *Syrphus balteatus* (Deg.), collected from the leaves of black poplar (*Populus nigra*) on which were both galls of *T. affinis* and *Pemphigus bursarius*, were found able to enter the mature galls of the latter and consume the contents. It is not known which species of aphid was the original prey.

Anthocorids.

Anthocorids are the major predators of *P. bursarius* when the galls have opened. Börner & Heinze (1957) gave *Orius* (cited as *Triphleps*) *minutus* (L.) as a predator, and Villiers (1945) stated that *Anthocoris nemorum* (L.) fed on aphids on poplar. The species found within galls of *P. bursarius* near Wellesbourne and elsewhere are *A. nemorum* and *A. nemoralis* (F.).

The effects of Anthocorids on the gall stage of *P. bursarius* were first observed when no fundatrigeniae emerged from a large gall collected from Stratford on 2nd July 1956. On opening up this gall, two adults of *A. nemorum* were found amidst the remains of the aphid contents. The remains had become aggregated into a bolus which had the sweetish smell of fermenting honeydew and on which fungus was beginning to grow. Subsequently, in 1956, many other galls were found to contain Anthocorid nymphs in various stages of maturity and their aphid victims

in various post-mortem stages. After mid-July, about 14 days after the beginning of gall opening, between 90 and 100 per cent. of all galls examined from poplar sites near Wellesbourne were attacked by Anthocorids. Galls to a height of 16 ft. up the trees were found to be affected to this same high degree. On some trees, galls were present to a height of 35 to 40 ft., and Anthocorids seemed to be active in these also, for there was a marked absence on the lower foliage of speckling by honeydew and wax which 'rains' down from the mouths of healthy galls.

Galls containing Anthocorids become recognisable by the altered appearance of the gall mouth. The emergence hole, instead of being small and round with thick wax-powdered lips, is relatively large, and irregularly shaped while the lips are thin and dark in colour with no wax coating.

Usually only one Anthocorid nymph or adult is found in a gall, but two or more may occur. The entire aphid contents of the gall are killed before the Anthocorid begins feeding. The killing is accomplished in an extremely short space of time, and if galls, recently opened and containing an Anthocorid nymph, are examined, all aphids regardless of size will invariably be dead and in a relaxed, undamaged condition. An idea of the efficiency with which the aphids are killed can be gained from the figures given in Tables I and I A. The figures were obtained from 30 galls containing Anthocorid nymphs, which were collected at random from the same site. The gall mouths could only have been open within a day or two of the examination being made, and the aphids were in a freshly killed condition.

Mode of killing by Anthocorids.—Whilst discussing this wholesale killing of *P. bursarius* with Dr. T. R. E. Southwood, it was suggested that a secretion from the stink glands possessed by Anthocorids might have the effect, within the confines of a gall, of killing the aphids by fumigation. If this 'gas chamber' idea is in fact the method by which *P. bursarius* is killed, it is quite novel, though it seems to be the most feasible explanation.

In galls recently entered by Anthocorids, examination of the freshly dead aphids (including the smallest first-instar nymph) has always failed to show evidence of external injury and, even if the aphids were killed by the same means as that used by Cecidomyiid larvae, the task of individually killing them all when they are so tightly packed within a gall would scarcely meet with complete success. The whole process is one of speed, and, if killed singly, some of the smaller aphids would undoubtedly be overlooked, whilst in going round from aphid to aphid the disturbance created by the predator would most likely cause some aphids to wander and crawl out of the gall; this has never been observed to happen.

The possibility that the female Anthocorid lays an egg within the gall, having first killed the contents by fumigation, cannot be excluded. However, Sands (1957) stated that the eggs of *A. nemoralis* and of *A. nemorum*, which are laid in plant tissue, have an incubation period of about seven days. This length of time appears to indicate that the egg is laid outside the gall and that, having entered, the first instar-nymph is itself able to kill the contents of the gall, for a gall, the mouth of which has opened considerably more recently than seven days, may contain a first-instar Anthocorid nymph and aphids so freshly affected that some are not quite dead and are still twitching.

Seasonal variation in attack by Anthocorids.—Four years' observations on *P. bursarius* on poplars around Wellesbourne have shown an interesting cycle of Anthocorid abundance.

In 1955, galls of *P. bursarius* were extremely abundant but, because Anthocorids were scarce, most of them remained free from attack. However, the predators were able to build up their numbers in such a plentiful host supply and a much increased Anthocorid population overwintered on the poplars. In 1956, galls of *P. bursarius* were not as numerous as in the previous year but were

still very common; the Anthocorid numbers built up further and the attack on *P. bursarius* became so intense (see above) that the migration period of the fundatrigeniae was curtailed by about two weeks. In 1957, Anthocorids were common but there were few galls of *P. bursarius*. When the latter opened they were

TABLE I.

Mortality of *P. bursarius* in galls following attacks by Anthocorids.

Gall	Numbers of dead aphids			Total
	Fundatrix	Fundatrigeniae		
		mature	immature	
1	1	14	120	135
2	1	12	72	85
3	1	10	77	88
4	1	13	67	81
5	1	24	69	94
6	1	7	71	79
7	1	8	66	75
8	1	9	43	53
9	1	22	107	130
10	1	11	67	79
11	1	14	84	99
12	1	16	188	205
13	1	11	101	113
14	1	5	15	21
15	1	15	92	108
16	1	14	117	132
17	1	15	89	105
18	1	12	86	99
19	1	13	100	114
20	1	9	23	32
21	1	17	106	124
22	1	10	138	149
23	1	17	117	135
mean				101

TABLE I A.

Analysis of the contents of seven galls of *P. bursarius* affected by Anthocorids, showing the numbers and sizes of the dead aphids.

Gall	Numbers of dead aphids					
	Fundatrix	Fundatrigeniae				Total
		mature	4th instar	3rd instar	2nd & 1st instar	
24	1	22	47	63	41	174
25	1	7	34	14	38	94
26	1	18	40	38	35	132
27	1	15	42	55	23	136
28	1	14	50	62	47	174
29	1	20	35	12	18	86
30	1	8	25	31	16	81
mean						125

quickly entered by the predators, and after the first week of July no galls containing living aphids could be found. The duration and strength of the aphid migration was thus considerably affected. Predator food supply must soon have become depleted and probably few Anthocorid nymphs survived to maturity. In 1958, there were extremely small numbers of galls of *P. bursarius* but repeated examination of these throughout July failed to reveal any attacked by Anthocorids. It is presumed, therefore, that the Anthocorids which did not die of starvation in 1957 moved from poplar in search of other aphids.

Predators of P. bursarius on lettuce.

A. Predators of the fundatrigeniae.

In 1956, 1957 and 1958, ladybirds were observed to feed on immigrant fundatrigeniae of *P. bursarius* which had alighted on lettuce foliage to produce their young. These ladybirds (*Coccinella septempunctata* L. and *C. undecimpunctata* L.) were on the lettuce preying on *Nasonovia ribis-nigri* (Mosley) when the spring migrants of *P. bursarius* began arriving. They were especially numerous in 1957 and must have substantially reduced colonisation by lettuce root aphid.

Following infestations of *N. ribis-nigri*, the larvae of *Syrphus* spp., including those of *S. balteatus*, have been seen on lettuce foliage when fundatrigeniae of *P. bursarius* were migrating into the crops. These larvae are far from specific in their choice of aphid host and they would probably consume any individuals of *P. bursarius* they encountered.

B. Predators of the alienicolae.

The colonies formed by *P. bursarius* on reaching the roots of lettuce are liable to attack from predators belonging to the Dipterous family CHLOROPIDAE and to the Coleopterous families CARABIDAE and STAPHYLINIDAE.

Balachowsky & Mesnil (1935) recorded the larvae of the Chloropids, *Thaumatomyia glabra* (Mg.) and *T. notata* (Mg.) (cited as *Chloropisca*) feeding in numbers on *P. bursarius* which was colonising the roots of *Sonchus* spp. These authors gave descriptions of the larvae and also characters whereby the two species can be separated. During the present work the larvae of both species have been found commonly among root infestations of *P. bursarius* and it is apparent that they are important predators of this aphid.

Parker (1918) described the life-history and habits of *T. glabra*, which he claimed was "by far the most effective enemy of the sugar beet louse (*Pemphigus betae* Doane)." He gave the aphid consumption of the larva and thought that under field conditions each larva, from eclosion to pupation, would probably consume about 75 aphids. He considered the fly to be largely univoltine, winter being passed as a puparium in the soil. Balachowsky & Mesnil (*op. cit.*), however, said there appeared to be two generations in France. In Britain also there appear to be two generations and even a partial third generation may occur. At Wellesbourne in 1957, for example, *T. glabra* went through one generation before the end of June on an infestation of *P. bursarius* which had built up on the roots of March-planted lettuce from apterae hibernating in the soil. What seemed to be a second generation of *T. glabra* then developed on colonies of *P. bursarius* which fundatrigeniae had founded on lettuce during July. The larvae of this predator were again found among autumn populations of *P. bursarius* on the roots of *Sonchus asper* and *Lapsana communis*, and puparia appeared in October and November.

Apart from the larger Carabid ground-beetles of the genera *Pterostichus* and *Harpalus*, which were occasionally found in the soil near infestations of *Pemphigus bursarius*, *Trechus quadristriatus* (Schr.) and *T. obtusus* Erichs. were commonly

found among colonies of this aphid and are strongly suspected of being predators on it.

The following Staphylinid adults have often been found in very close association with *P. bursarius* colonies on lettuce roots:—*Atheta* spp.; *Aleochara* spp.; *Oxytelus rugosus* (F.); members of the PAEDERINAE; *Tachinus rufipes* (Deg.) and *Tachyporus chrysomelinus* (L.).

The larvae of several species of Staphylinids have also been found in colonies of *P. bursarius*; some of them undoubtedly belong to the above genera and are probably the young of some of the species listed. Adults of *O. rugosus* and *T. chrysomelinus* occurred commonly and the orange-yellow larvae and pupae of the latter species were often found whilst sampling aphid-infested root systems.

Coleoptera as predators of P. bursarius.—Of all the Coleoptera found associated with *P. bursarius* in the soil, only the larvae of one, *T. chrysomelinus*, have been observed feeding on the aphid. This is not surprising, for examination of an aphid colony on the roots of lettuce disturbs the beetles, which immediately cease feeding and try to hide away. However, many Carabids and Staphylinids are known to be general predators with a wide host range, and with such lack of specificity, root aphids, being soft-bodied and relatively immobile, are likely to fall easy victims to such beetles in search of prey. Furthermore, because one species has been seen feeding on *P. bursarius*, and *T. obtusus* has been recorded as predacious on the strawberry aphid, *Capitophorus fragaefolii* (Ckll.) (cited as *C. fragariae* (Theo.)) (Dicker, 1944), there seems to be little doubt that the Coleoptera found associated with *P. bursarius* are predators on it.

The effect of predators on subterranean populations of P. bursarius.—Despite lack of observations on actual feeding, the combined effect of predators has been seen many times during August and later. Often all that remained of what was, or might have been, a large colony of several thousand aphids were traces of wax and occasionally a few dead aphids.

However, like most predators on aphids, those affecting *P. bursarius* generally appear after the host has already begun to build up its numbers and, although they may check and eventually eradicate the host population, they seldom prevent colonisation, and, if weather conditions permit a high rate of aphid increase, plant damage invariably results before the predators can gain the ascendancy.

C. Enemies of the sexuparae.

From about mid-August when potential sexuparae have begun to aggregate around the base of the host-plant to form wings and migrate, they can be preyed upon by ladybirds and Syrphid larvae and are often attacked by entomogenous fungi.

Adults of *Coccinella septempunctata*, *C. undecimpunctata* and *Adalia bipunctata* (L.) have been found on lettuce plots at Wellesbourne at the time when sexuparae were developing, and an individual of the first species was found actively moving over lettuce foliage as late as 11th October. This ladybird readily consumed winged sexuparae of *P. bursarius* when brought in to the laboratory and, at 69°F., ate a daily average of 15. The larvae of the Syrphid, *Melanostoma mellinum* (L.), have also been seen on lettuce foliage in late August and early September. They were probably feeding on maturing sexuparae of *P. bursarius*.

Fungal disease can reach epidemic proportions and decimate entire populations of sexuparae should conditions of humidity and temperature be favourable. Rockwood (1950), stated that the spores of *Empusa aphidis* were discharged when the relative humidity at night was 90 per cent. or more. In late August and in September the relative humidity must almost constantly exceed 90 per cent. under the lower leaves of lettuce; thus entomogenous fungi are potentially much more important in controlling the sexuparae than are predators.

In 1955, fungal disease killed most of the populations of *P. bursarius* (chiefly maturing sexuparae) during the third and last week in August. It was noticeable that in fields where irrigation had been practised the epidemic spread more rapidly.

Predators of the sexuparae on poplar.

Sexuparae that succeed in migrating back to poplar are liable to be attacked by ladybirds and Anthocorids while they are searching for, or are located in, bark crevices. This could also apply to the sexuales of *P. bursarius*, although their small size must make them less easy to locate than the sexuparae.

Adults of *Coccinella undecimpunctata*, *Adalia bipunctata*, *Anthocoris nemorum* and *A. nemoralis* have all been found hibernating in bark crevices on Lombardy poplars, and on warm autumn days preceding hibernation they were often observed scouring the bark for prey. *Adalia bipunctata* occurred most frequently, and on a sunny October day as many as 8 were counted on the trunk of one poplar tree. The number of sexuparae consumed daily by this species of ladybird was recorded at three different constant temperatures within the range of those usually experienced outdoors in autumn. The results showed that the consumption rate rose linearly with temperature, 4 sexuparae being consumed at 63°F., whilst feeding started at about 44°F. Sexuparae, however, begin to reproduce at 41°F. (Dunn, 1959) so that cool autumn days, with temperatures below 45°F. but above 40°F., benefit *P. bursarius* by preventing ladybird activity while enabling some aphid reproduction.

Summary.

Because the lettuce root aphid, *Pemphigus bursarius* (L.), is gall-inhabiting on poplar in spring and lives underground on lettuce during summer, its natural-enemy complex differs from that associated with foliage-feeding aphids. It suffers little from parasites and only fundatrices have been found attacked. The only species reared from parasitised individuals was the Pteromalid, *Pachyneuron* sp., which is assumed to be hyperparasitic. When the galls open at migration time, Syrphid larvae and Anthocorids can enter and attack the contents. *Anthocoris nemorum* (L.) and *A. nemoralis* (F.) are the main predators at this stage. Before they begin feeding, they kill all the aphids within a gall extremely quickly and efficiently. It is suggested that the aphids may be killed by a secretion from the stink glands of the Anthocorids working as a fumigant within the confines of the gall. Several Staphylinids and Carabids are frequently associated with subterranean colonies of *P. bursarius* and are almost certainly predators. The larvae of the Chloropids, *Thaumatomyia glabra* (Mg.) and *T. notata* (Mg.), are common predators of *P. bursarius* in the soil. The sexuparae, both before they leave the lettuce plants and on their arrival on poplar, are attacked by three species of Coccinellid.

References.

- BALACHOWSKY, A. & MESNIL, L. (1935). Les insectes nuisibles aux plantes cultivées . . . Tome premier.—1137 pp. Paris, Busson.
- BÖRNER, C. & HEINZE, K. (1957). Aphidina-Aphidoidea. In Sorauer, P. Handb. Pflanzenkr. 5. Aufl. 5 2.Teil. 4.Lief. Homoptera, II. Teil. pp. 1-402. Berlin, Parey.
- DICKER, G. H. L. (1944). *Tachyporus* (Col., Staphylinidae) larvae preying on aphides.—*Ent. mon. Mag.* 80 p. 71.
- DUNN, J. A. (1959). The biology of lettuce root aphid.—*Ann. appl. Biol.* 47 pp. 475-491.

- HEISS, E. M. (1938). A classification of the larvae and puparia of the Syrphidae of Illinois exclusive of aquatic forms.—*Illinois biol. Monogr.* **16** no. 4 (*Univ. Ill. Bull.* **36**) 142 pp.
- PARKER, J. R. (1918). The life history and habits of *Chloropisca glabra* Meig., a predaceous Oscinid (Chloropid).—*J. econ. Ent.* **11** pp. 368–380.
- ROBERTI, D. (1938). Contributi alla conoscenza degli afidi d'Italia. I. I pemfigini del pioppo.—*Boll. Lab. Zool. Portici* **30** pp. 169–238.
- ROCKWOOD, L. P. (1950). Entomogenous fungi of the family Entomophthoraceae in the Pacific Northwest.—*J. econ. Ent.* **43** pp. 704–707.
- SANDS, W. A. (1957). The immature stages of some British Anthocoridae (Hemiptera).—*Trans. R. ent. Soc. Lond.* **109** pp. 295–310.
- VILLIERS, A. (1945). Atlas des hémiptères de France. I. Hétéroptères gymnocérates.—*Nouv. Atlas Ent.* no. 4, 83 pp. Paris, Boubée.

THE WHITE COFFEE BORER, *ANTHORES LEUCONOTUS* PASC., AND ITS CONTROL.

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(PLATE IX.)

Anthores leuconotus Pasc., the white coffee borer, has been an important pest of *arabica* coffee for over 80 years. In Tanganyika, the insect destroyed hundreds of thousands of coffee trees in the lower coffee-growing areas, and during the post-war years the insect appeared regularly in the higher elevations where hitherto it had not been observed. Attempts to control the beetle by hand operations were tedious and expensive and rarely satisfactory. An investigation was initiated in 1950 to find an efficient and economic control measure, and by 1955 a dieldrin treatment applied to the stems had been developed and proven to be satisfactory. Today (1958) the borer has been reduced to insignificant numbers wherever control measures have been undertaken.

Distribution.

A. leuconotus is found and believed to be indigenous in Central, East, South and South-West Africa, including Angola, Belgian Congo, Cameroons, Kenya, Mozambique, Natal, Northern Rhodesia, Nyasaland, Southern Rhodesia, Tanganyika, Transvaal, Uganda and Zanzibar (Duffy, 1957).

In Tanganyika, the species can be found in almost all the areas where *arabica* coffee is grown including the Usambara and Pare Mountains (Tanga Province), Kilimanjaro, Meru and Oldeani (Northern Province), Bukoba (Lake Province), Mbozi and Rungwe (Southern Highlands Province), Matengo (Southern Province), and in the Uluguru Mountains (Eastern Province).

Life-cycle.

Pascoe (1869) first described the beetle, and Gooch (1874) gave the first account of its habits and life-cycle on coffee in Natal. Fuller (1901) stated that *A. leuconotus* and coffee leaf rust, *Hemileia vastatrix*, contributed largely to the fall of the Natal coffee industry. Morstatt (1912) reviewed all that was known of the pest, and added his own observations. In Kenya, James (1928) gave an account of his observations, and Knight (1939) gave additional details of the life-cycle and recommended control measures. In Tanganyika, Ritchie (1933) in the early thirties recommended control measures for use in the Northern Province of Tanganyika, and discovered five species of wild host trees. A fuller account of this work was published by Davies (1937). Moffat & Allan (1934) published an account of the biology as observed at Abercorn, Northern Rhodesia; and Lewin (1936) added to their observations. Gardner (1934) briefly described the larvae. Morstatt (1935), Lepesme & Villiers (1944), Chevalier (1947) and Duffy (1957) reviewed the biology of *A. leuconotus*, and Duffy described the beetle, pupal and larval stages.

Very little new work on the biology or control of *A. leuconotus* has been published since 1939 except in Annual Reports of the author (Tapley, 1952-1958), and in Tanganyika Coffee Board pamphlets (Tapley, 1955c, 1957).

The egg.

The egg is light cream in colour, approximately $5\frac{1}{2}$ mm. long by 2 mm. in diameter, tapering at each end. The anterior of the egg is blunt and the posterior attenuated (Knight, 1939). The chorion is smooth, tough and flexible.

Incubation takes from 21 to 23 days in the laboratory at Lyamungu, which agrees with Knight's observation of 20 to 23 days at 4,200 ft. in Kenya. Moffat & Allan (1934) state that the incubation period in Northern Rhodesia is apparently less than ten days, but Lewin (1936) observed it to be 20 to 30 days.

The larva.

The larva passes through two phases: in the first it feeds on the soft tissue of the cambium and phloem while boring under the bark, and in the second it bores inside the hard wood.

For the first few days after hatching, the larvae remain feeding in the egg cavity, and then begin to tunnel extensively in the bast between the wood and bark. If the eggs from which they originate were laid (as most are) within a few inches of ground-level the larvae invariably burrow directly down the tree to below ground-level and then ring-bark the bole and main roots. Where eggs are placed higher up the tree, the larvae girdle the tree forthwith and do not attempt to reach the roots. The extent of the damage caused by one ring-barking larva is shown in Plate IX, fig. 1.

The ring-barking larvae can only be detected with difficulty, since the bark remains largely undisturbed. Sometimes a minute piece of frass protruding from the hole through which the egg was laid affords a clue. The superficial burrows become obvious only when the wood-boring larvae fill them so full that the bark bulges and eventually the cream-coloured frass spills.

Knight (1939) states that the larva burrows about one inch in the first month and about four inches in the next three weeks. Thereafter it may move about a quarter of an inch a day, and tunnel for some 20 inches before entering the wood.

When the larvae are three or four months old, they burrow into the wood of the tree. A wood-boring larva can be observed working in a burrow by cutting a plane surface on the stem of a coffee tree, chiselling out a burrow in it approximately the size of the burrow from which the larva has been taken, and screwing a 'perspex' sheet over the artificial burrow. The larva is then introduced into it. If the larva is observed in very dim, indirect light, and otherwise kept in darkness, it may remain visible for weeks, but eventually bores away from the perspex or covers it with frass. (Pl. IX, fig. 2.)

In this way the excavation of tunnels was observed. A larva anchors itself in the tunnel and rasps away the end grain of the wood with its mandibles, producing a wood dust. The burrows are enlarged laterally by the larva seizing a bundle of wood tissue and stripping it from the wall of the tunnel, thus producing the frass, which protrudes loosely from the entrance. Faecal matter appears as cylindrical pellets which may later disintegrate. Apparently the larvae feed only to a limited extent on the wood excavated to form the burrow.

Towards the end of the wood-boring phase the larva changes its appearance. Organs partly visible through the semi-transparent skin become completely masked with fatty tissue. A pupal chamber (Pl. IX, fig. 4) is excavated at the top of the burrow, adjacent to the bark, and the frass from it is tightly packed in the entrance.

It proved impracticable to determine the number of larval instars by direct observation. The mean head-capsule width of 60 first-instar larvae shortly after eclosion was 0.98 mm., and the mean head-capsule width of 80 larvae which were believed to be in the second instar was 1.27 mm., the ratio of the second to the first being 1.29:1.

Two larvae were found with their exuviae, and the ratio of increase was found to be 1.32 and 1.31, the actual measurements being 1.67 mm., 2.20 mm. (ratio 1.32) and 1.93 mm., 2.53 mm. (ratio 1.31), respectively.

The head-width measurements of 362 pupating larvae obtained in a survey from Moshi and Arusha districts gave a mean of 4.45 mm. with a standard deviation of 0.48 mm., a standard error of 0.025 mm. and a coefficient of variation of 10.8 per cent.



Fig. 1.—Histogram showing the sizes of head capsules of larvae of *A. leuconotus* taken from *arabica* coffee during a survey made at regular intervals over a period of 18 months in the Moshi and Arusha districts. Some of the early instars were taken from experimental plots.

By applying Dyar's law which appears to be applicable to at least one other Cerambycid beetle (Duffy, 1946), and knowing the first, second and final instar head-widths it can be concluded that there are probably seven instars with mean head sizes as follows:—0.98 mm., 1.27 mm., 1.6 mm., 2.1 mm., 2.7 mm., 3.5 mm., 4.5 mm.

A histogram (fig. 1) of all head measurements of larvae obtained from a survey of Moshi and Arusha districts (mainly later stadia) and from experiments (mainly early stadia), but excluding the 60 first- and 80 second-instar larvae already mentioned, confirms that the head capsule of the first-stage larva measures from 0.9 mm. to 1.0 mm., and of the second 1.2 mm. to 1.3 mm. A third peak expected at 1.6 mm. to 1.7 mm. does not appear, but there is a slight peak at 1.9 mm. which may be the third instar, and another peak, which may represent the fourth instar, appears at 2.3 mm. The fifth may be represented at a peak at 2.7 and the sixth by another peak at 3.6 mm. If this is the case the last instar, with a head-capsule width of 4.45 mm., must be the seventh.

Growth of the larvae and larval instars.

Coffee trees at Lyamungu were infested by introducing beetles into cages, 1 cubic ft. in size, placed round the stem during the short rains of 1953/54 and long rains of 1954 (Pl. IX, fig. 3). The beetles laid freely in the cages and the date of oviposition was noted. Where too many eggs were laid in one tree some were removed, and the others were left to produce larvae. At set times

after oviposition, when trees were uprooted and the borers dissected out, the head capsule of each larva was measured. Altogether 168 larvae were measured in this way and a further 60 first-instar larvae were measured as they emerged from eggs in the laboratory.

A graph of the age of the larvae in weeks from oviposition against the minimum diameter of head capsules showed clearly that growth of the early instars was much faster than of the later instars. In fact the mean weekly growth from the third to the 28th week was 0.12 mm., whereas from the 28th week to 63rd week after oviposition the growth was reduced to a mean of 0.033 mm. per week.

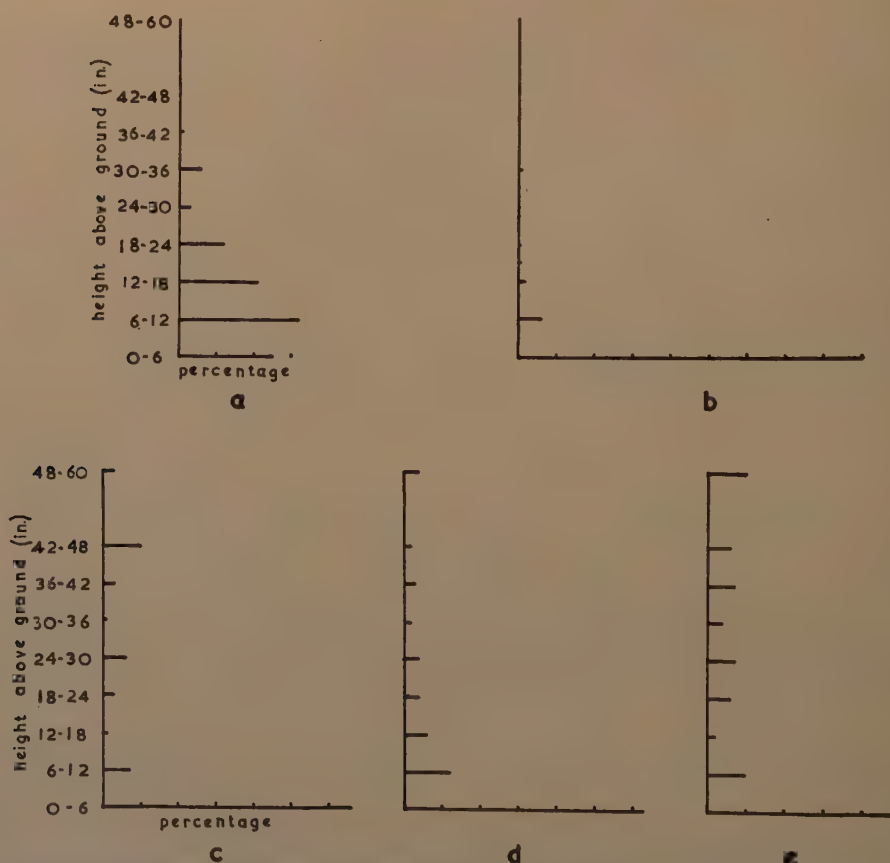


Fig. 2.—Histograms showing the distribution of egg sites and beetle emergence holes of *A. leuconotus* in stems of *arabica* coffee. The upright of each histogram represents the coffee stem marked at different levels from the ground, and the horizontal lines represent the number of egg sites or emergence holes at each level of the stem as a percentage of the total found. Each mark on the lower line represents 10 units. (a) distribution of oviposition sites on stems at the Coffee Research Station, where 251 egg sites were observed; (b-e) distribution of emergence holes on stems in heavily infested areas of Mt. Kilimanjaro. Mean number of emergence holes per tree for each area is shown below in brackets: (b) East Kilimanjaro (1.2); (c) South Kilimanjaro (1.4); (d) South Kilimanjaro (4.5); (e) South Kilimanjaro (4.0).

Larval positions in the coffee tree.

It was observed that in the lower areas of the infested zone (below 4,000 ft.) most of the damage occurred at the base of the tree, and only a small number

of larvae lived above 18 in. in the main stem. At higher elevations (above 4,000 ft.) the bulk of larval infestation occurred higher above ground level. The pattern has not changed since before 1914 when Morstatt (1912) made similar observations.

At the Coffee Research Station (4,100–4,200 ft.), where borers were active in 1952, a survey was made of the positions at which eggs were laid in the main stem of shaded single-stem trees. Altogether 251 egg sites were observed, of which 90 per cent. were within two ft. of soil level but very few actually near the soil. The distribution is shown in fig. 2, a.

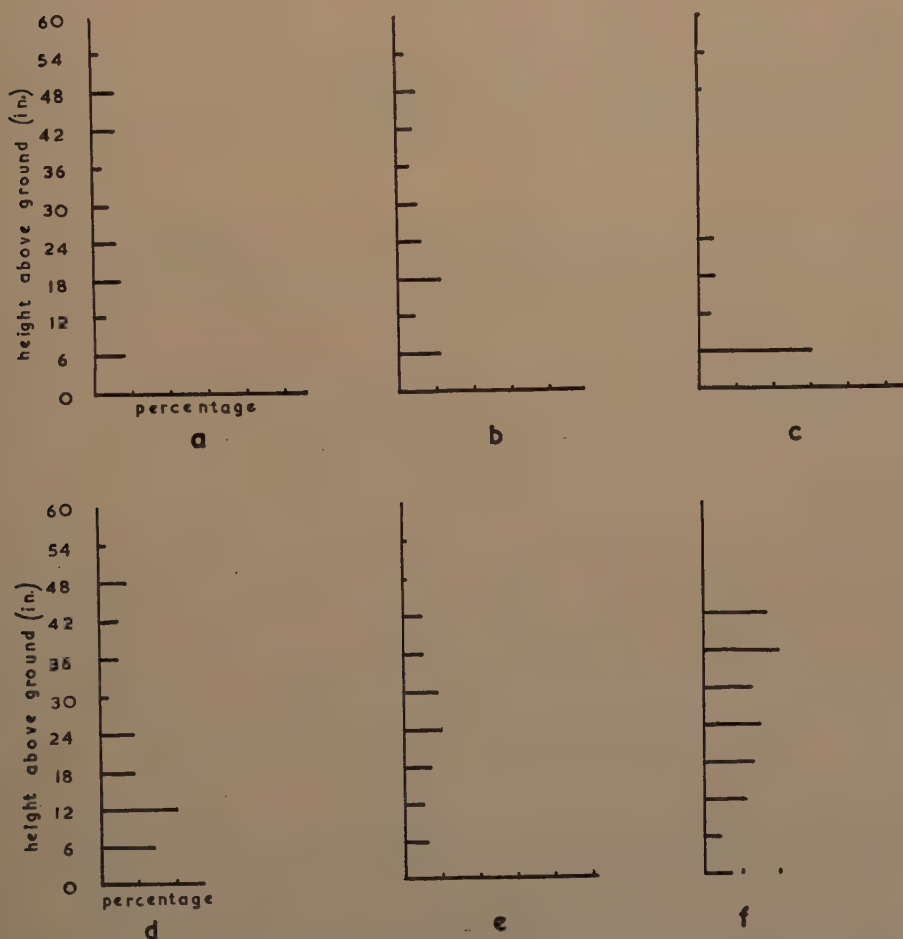


Fig. 3.—Histograms showing the distribution of burrows of *A. leuconotus* in stems of *arabica* coffee at different altitudes on Mt. Kilimanjaro. For method of presentation see fig. 2. (a) 3,300 ft.; (b) 3,400 ft.; (c) 3,800 ft.; (d) 3,900 ft.; (e) 4,300 ft.; (f) 4,500 ft.

In other areas, where it was not possible to observe egg positions, the distribution either of emergence holes or of burrows was noted. Where trees could be uprooted, cuts were made at six-inch intervals along the stem and the number of burrows at each level recorded. The results for emergence holes and burrows are presented graphically in fig. 2, b–e and fig. 3, a–f, respectively. In

five of the six sites investigated for burrows, 74 per cent. of these were found in the lower 18 in. of the stem, and 82 per cent. in the lower 24 in. The remaining burrows were more or less evenly distributed in the rest of the stem. In the sixth site, an estate at 4,500 ft. at Sanya Juu, only 35 per cent. of the burrows were located in the lower 18 in. of stem.

In the areas of Kilimanjaro where the distribution of emergence holes was studied, a total of 78 per cent. of all emergence holes occurred in the lower 2 ft. of stem, most of which (62 per cent. of the grand total) were found in the lower 6 in. of stem (see fig. 2, b-e). The remainder were more or less evenly distributed in the rest of the stem. Where the infestation was light, at about one emergence hole per tree, there were apparently fewer borers at the top of the trees than when the infestation was heavy, at about four emergence holes per tree.

In the case of multiple-stem trees only the base of the tree is suitable for borers and larvae are rarely found in the primary branches.

At Mbozi, in the Southern Highlands Province, practically all borer larvae live in the base of the tree, and it is comparatively rare to see burrows in the upper parts.

The pupa.

Pupation takes place in the pupal chamber which is prepared just inside the bark. Pupae are always found with the head uppermost in the chamber.

In a survey made in the Northern Province, female pupae were found to be significantly heavier than male pupae. The mean weight of the female pupa was 1.23 g., and that of the male was 0.99 g.

James (1928) reports that the pupal stage lasts 38-42 days, and a further two or three weeks elapse before the adults emerge from the pupal cell. Moffat & Allan (1934) give the pupal period as being 20 to 30 days.

Observations made at Moshi suggest that the pupal period is 4 to 4½ weeks, and that the beetle remains in the tree for nearly a further two weeks.

The adult.

The adult emerges from the pupal chamber by biting a circular hole, about 1 cm. in diameter, in the bark. This has been observed in the field on a few occasions in daylight, when attention has been drawn to it by a distinct rustling noise. The beetles emerge with deliberation, and then walk up the main stem to the uppermost part of the canopy where they rest and feed on green tissue of branches, and sometimes at the base of the leaf and of the cherry. The damage so caused, even where infestations are heavy, is negligible.

Knight (1939) stated that males are more numerous in Kenya during the early part of the main period of adult emergence, and this was confirmed in Moshi district. A flush of beetles was observed during 1952. Beetles were first noticed on 21st March and they disappeared after 17th May. Regular collections of beetles were made during this time. From 21st March to 9th April 507 males and 277 females were collected, and from 15th April until 17th May 225 males and 484 females. It is apparent that during the whole flush the sexes were approximately equal, the ratio of 732 males to 761 females not being significantly different from the 1:1 ratio. The data given by Knight, which suggest that males outnumber females, are to be interpreted in the light of the fact that they were derived merely from parts of two flushes.

Female beetles are slow, sluggish insects and spend their time on the upper branches of a tree feeding or resting. The males are active in searching for females. If disturbed, beetles will either make a rasping noise by rubbing the prothorax against the mesothorax, or drop from the tree. Flight, in daylight at least, can only be induced by placing large numbers of beetles in a confined space. Nothing will induce a solitary insect to fly or walk, which was found to

be a disadvantage in insecticide assay work (Foster, 1955). However, in the field, beetles have been observed to fly a distance ranging from a few feet to about 100 yards. It is believed that some beetles can fly up to a mile, since several isolated groups of about 20 coffee trees in plantations, one mile from the nearest known source of infestation, have been observed to contain larvae resulting apparently from the oviposition by a single female.

Copulation takes place soon after emergence from the tree and may take from one to several hours. Copulation is frequent and continues through the season until the males have disappeared. Oviposition takes place several days after mating, but Moffat & Allan (1934) found the preoviposition period to be 30 days.

The number of eggs which can be laid by a female beetle was stated by Knight (1939) to be 40, and by Moffat & Allan (1934) to be 26. No additional observations were made at Lyamungu, but during the warm weather of the short rains, from November to January, caged females have been known to lay four eggs in a 24-hour period. During the cold, wet and overcast conditions of May and June, caged females may lay only one egg in five days. Female beetles live for 6-8 weeks.

Knight (1939) states that eggs are mostly laid in darkness. At Lyamungu, oviposition was found to take place mainly between sundown and midnight. When a female is ready to lay, she walks from the branches to the main stem and searches for a site, and may take from 5 to 30 minutes in doing so. She then bites away the bark with her mandibles, making a transverse, semicircular depression, until living tissue is reached. Approximately 20 sq. mm. of bark is removed, more or less depending on the depth of bark to be penetrated, and the process may take from 5 to 20 minutes. As far as could be determined, no feeding takes place at this time. Frequently a site is abandoned before completion, and a new one selected. While preparing the site, the head of the beetle is always facing down the tree, but for oviposition the female always faces upwards. The ovipositor, which is strongly sclerotised and is normally retracted within the abdomen, is inserted upwards in the cambium region; it lifts the bark and forms a cavity in which the egg is deposited. Eggs are deposited with the posterior (more acute) end uppermost. The female expends considerable effort for about half a minute while inserting the ovipositor. The egg is deposited, and the hole in the bark is sealed with a brown substance which appears to be allied to chitin. Eggs are laid singly; only once have two eggs been observed together in one chamber. Actual oviposition was observed to take from 10 to 12 minutes, and in one extreme instance as long as 27 minutes. Knight states the time of preparation and oviposition to be only 5 to 8 minutes.

Duration of life-cycle.

Morstatt (1912) working at Amani (Usambara Mountains) states that most individuals complete their cycle in the tree during a two-year period, while others may do so in 18 months. Moffat & Allan (1934) state that the duration from egg to adult is at least 23 months in Northern Rhodesia, where coffee is infested up to an altitude of 5,400 ft. Smee (1927) states that, in Nyasaland, the larvae work at least two years in the stem, and Anderson (1928) states that, in Kenya, it is considerably less than two years, while Knight (1939) also estimates its cycle in Kenya at two years.

The duration of the life-cycle in the field is difficult to estimate. However, in a survey made in Moshi district, a cycle from pupating larvae, to pupae, beetles, ring-barking larvae, wood-boring larvae and to pupating larvae again was followed closely. The details follow:—

By August 1954 about 50 per cent. of all larvae were preparing pupal chambers and the borers pupated in September and to a lesser extent through to February.

Beetles were found in the trees early in November, December and January; this was followed immediately by a peak of egg-laying which continued at a slower rate until June. Ring-barking larvae first appeared in large numbers in January and February and continued in lesser numbers until the end of June. A peak of wood-boring larvae appeared in April and May and continued through to February 1956 when they started to show signs of pupating. It was not possible to follow the cycle further, but it is likely that they pupated in large numbers during March and April since heavy egg-laying occurred in May and June 1956.

In the meantime another generation of larvae was preparing to pupate in July 1955 and they emerged as beetles to give a peak of egg-laying in January and February 1956.

It is well established that in the Moshi district there are two main periods of emergence of beetles each year, but the times and intensity may vary a little from year to year. The first flush is from November to January (short rains) and the second from April to June (long rains). Beetles can be found in small numbers at other times of the year except from August to October when they are rarely observed.

It would appear, therefore, that a generation starting in the short rains is completed in the long rains one year hence, and similarly a generation starting in the long rains is completed during the short rains one year hence. However, this is doubtless an over-simplification since it has been found at Lyamungu that individuals require from 12 months to 25 months to complete their life-cycle.

In the first of a series of observations, on a total population of 77 individuals, 6 beetles reached the adult stage 12 or 13 months after oviposition. When, 11½ to 14 months after oviposition, the trees were uprooted and dissected, another 19 beetles were found ready for emergence, together with 6 pupae and 36 larvae. Nine larvae and one beetle had died.

In the second of a series of observations, eggs were laid in trees during the long rains from late March to mid-May in 1952. Of a population of 42 individuals that completed their life-cycle, 6 males and 1 female emerged during the following long rains after 12 to 14 months, 12 males and 18 females in the short rains of 1953 after 16½ to 19½ months in the tree and a further 2 males and 3 females during the April of the long rains of 1954 after a period of 23½ to 25 months.

In a third series of observations, on insectary-reared individuals, four beetles emerged after 18 months, four after 19 months and three more after 23 months. Of nine individuals maintained in a cage at approximately 27°C. all emerged after 13½ months to 15½ months in the trees.

In conclusion, it can be stated that the life-cycle of *A. leuconotus* covers one to two years, but most individuals complete their development in 16 to 20 months.

Duration of the different stages of the life-cycle within the coffee tree.

From August 1954 to February 1956, 518 coffee trees were uprooted at more or less regular intervals from three badly infested estates in Moshi district. (The survey was not continued after February as control measures were applied or the trees were uprooted.)

The 518 trees were brought to the laboratory where they were carefully examined for eggs, ring-barking larvae (RB), wood-boring larvae (except final stage) (WB), final-instar larvae preparing the pupal chamber (PL), pupae (P) and adults (B). In all, 1,552 individuals (about three per tree) were found, comprising 69 eggs, 320 ring-barking larvae, 836 wood-boring larvae, 202 final-instar larvae, 90 pupae and 35 adults.

As the survey extended over a period approximately equal to that of one life-cycle, it might be expected that the total number of each stage present would

be proportional to the duration of that stage. If the mean cycle is 18 months then the theoretical duration of each stage is as shown in Table I.

It is difficult to know precisely how long ring-barking continues since many individuals which have prepared burrows in the wood have been caught feeding on the soft outer tissues. Evidently the change from feeding on the bast to the wood is not sudden, but may take several weeks to complete.

Natural mortality.

The toll of borer population by natural factors is very considerable, and it appears that only one of every four eggs laid ever develops into a living beetle.

Almost all eggs hatch normally. A very few have been found parasitised by a Eulophid, *Aprostocetus* sp. These parasites are extremely small, and up to eleven have been observed to emerge from one host egg.

TABLE I.

The theoretical and observed duration (in weeks) of the different stages in the development of *A. leuconotus*.

	Egg	RB	WB	PL	P	B
Calculated on basis of 18 months	3½	16	42	10	4½	1½
Observed directly	3-3½	13-17	—	—	—	—

Ring-barking larvae appear to be very susceptible to parasite activity, and when dissecting trees a large number of incomplete burrows are nearly always observed. In the untreated plots of an extensive chemical control experiment in Moshi district, where trees were examined for ring-barking larvae, a total of 530 fresh burrows were found, of which 368 contained living larvae, while the other 162 burrows were empty, contained dead larvae or, in 9 cases, parasitised larvae. Hence the mortality here was about 31 per cent., but in Arusha district, where a total of 542 burrows were examined, mortality was only 7 per cent. Had the larvae been left undisturbed, doubtless the mortality would have been higher, perhaps as much as 50 per cent.

The causes of mortality are not fully known, but insect parasites do play a part. Five species are believed to attack ring-barking larvae; these comprise three Pteromalids, two belonging to undetermined genera near *Dimachus* and *Dinarmus* and the third to an undetermined Cheilopachine genus, a species belonging to *Ceratoteleia* (SCELIONIDAE) and a species of *Tetrastichus* (EULOPHIDAE).

Unfortunately the number of adults obtained was very small, but the number of empty parasite pupal cases found in the burrows was considerable.

An assessment of the mortality of wood-boring larvae was made in one plot of coffee in which borer control had been almost completely neglected. Fifty trees were uprooted and all burrows carefully examined. Altogether 424 burrows were found, of which 37 contained living larvae. Of the remainder, 196 burrows had pupal chambers and emergence holes indicating that the beetles had developed normally and escaped from the trees. Another 160 burrows were incomplete, indicating that the larvae or pupae died from natural causes. A further 31 larvae appeared to have died as a result of control measures since the burrows showed signs of having been broken into with chisels.

Disregarding the burrows containing living larvae, and damaged burrows, it could be safely inferred that approximately 45 per cent. of the total population

over the years had not reached maturity. This figure derived from one plot of coffee is believed to be fairly typical of mortality as a whole. Of many hundreds of trees examined from all parts of Moshi, Arusha and Mbozi, the number of incomplete burrows was always numerous. In Kenya, Knight (1939) reports that the Braconid, *Iphiaulax varipalpis* Cam. destroyed about 48 per cent. of the larvae in the cases that he quotes.

The causes of mortality are not known. Certainly many of the deaths were caused by parasites, three species of which have actually been removed from the burrows. These have been determined as being the Ichneumonid species, *Afrocoelichneumon didymatus* (Morl.), *Cratichneumon* sp., and *Nadia* sp. nr. *ruficeps* (Cam.).

In Kenya, Knight states that a woodpecker preyed on borer larvae in *Gardenia urcelliformis*. Mayné (1923) reports that an ant, *Odontomachus haematodes* (L.), devours larvae in their galleries.

In some cases, beetles have been found dead in pupal chambers, possibly having been unable to extricate themselves from the tree.

Beetles that have emerged from the trees seem to be free of natural enemies and no external parasites have been observed.

The rise of populations of *A. leuconotus*.

During the first decade of this century, *A. leuconotus* appeared at scattered points in the middle of the coffee belt (Morstatt, 1912), but the distribution was very irregular, frequently being confined to single estates, or even parts of estates. From the established centres the beetles moved down the mountain to the lower estates, and also gradually moved up to higher elevations. The slow but sure rate of progress can be illustrated by reference to Uru just north of Moshi town. The beetle was well established at 3,500 ft. in 1928, and by 1932 it was operating at 4,000 ft. By 1950, coffee as high as 4,400 ft. was heavily infested and by 1952 there were already small groups of active larvae above this level. In 1955, the borer could be found at 4,600 ft.

A survey made in 1950 showed that the upper limit of the 'borer belt' on Kilimanjaro was approximately 5,000 ft. at Mkuu and Kilema, 4,400 ft. at Kirua, Old Moshi, Uru and Kibosho, 4,100 ft. at Lyamungu, 3,900 ft. at Machame and then up to 4,800 ft. at Sanya. The lower limit of the belt was the lowest level at which coffee was grown except at Mkuu, 4,400 ft., where coffee that had not become infested could still be seen below the 'belt'.

The infestation advances on a general front, and by individual females alighting on coffee perhaps as much as one mile from the nearest known point of infestation. These females lay eggs in groups of 20 to 30 trees, which form the basis of extensive new infestations.

If the borer showed any early preference for coffee trees in favoured positions these were soon lost as populations rose. During the 1930's, control measures, including the destruction of numerous wild hosts, apparently held the infestation in check. During the Second World War many immigrant agriculturists departed, leaving many farms in the hands of the Custodian of Enemy Property. During the post-war period, coffee farms once again assumed permanent ownership, but by this time many coffee trees were severely damaged by the borer. Borer populations had multiplied many times and it was quite apparent that control measures employed in the past would no longer be suitable. Trees were commonly found to harbour four or five larvae, and one tree, a record, was found to contain 37. Estate coffee was, on the whole, more severely damaged by borer than peasant-owned coffee, but nevertheless all coffee in the 'borer belt' was more or less affected seriously.

The acreage of coffee on Kilimanjaro that had been damaged by borer has not been assessed, but it is known that at one time most of the estates were

affected to a greater or lesser extent, and indeed many estates uprooted coffee as borer made production uneconomic. Probably about half of the African-owned coffee has been seriously affected.

It is perhaps surprising that the borer spread as slowly as it did, and took some 50 years to reach its present boundaries only a few miles from the original sources of infestation, and still apparently not at the limit of its potential development. Undoubtedly the sluggish habits of the beetles, its low rate of reproduction, the slow larval development coupled with high mortality factors, including the hand of man, have all contributed to an extremely slow dissemination rate.

The damage caused by *A. leuconotus*.

The loss of crop caused by the borer depends to some extent on the conditions under which the coffee grows. Trees which are grown in conditions near the optimum seem to suffer very much less than trees grown in less favoured conditions, such as in areas where rainfall is marginal, or where there is weed or heavy shade-tree competition.

At the Coffee Research Station, Lyamungu, the trees apparently suffer comparatively little from one or two larvae infesting the roots or stem, and injured superficial tissue soon heals. In one experiment observed at Lyamungu, the Single Tree Progeny Plot, an attempt was made to determine the loss of crop caused by a light infestation of one borer per tree, or more rarely two or three, on 14- to 15-year-old trees. The crop from 209 trees that were first infested in 1950 or 1951 was compared with the crop from 332 undamaged trees over the four-year period from 1951 to 1954. The trees were treated with insecticides and were not infested after 1951. The damaged trees yielded at the rate of 4.94 cwt. of clean coffee per year per acre, while the undamaged trees yield at 5.33 cwt. of clean coffee, giving a difference of approximately 0.4 cwt. which was significant at the 5 per cent. level. The loss, while not apparently very great, represented a figure approaching £10 per acre per year. The plot as a whole yielded poorly for Lyamungu.

It was not practicable to obtain comparable figures from other areas, but where populations approaching 6,000 borers per acre were always present (as happened in a few cases) the trees yielded very poorly, producing a small crop perhaps once in three years. Where populations were of more normal size, ranging from 500 to 1,000 per acre, the crop was estimated to be about 2-3 cwt. per acre per year. However, other factors are involved and it is impossible to estimate the accumulated losses over the years, but the figure doubtlessly amounts to millions of pounds.

The coffee borer very rarely kills mature coffee trees, even trees infested so heavily that the original root system has been completely destroyed. The reason for this seems to be the remarkable ability of the tree to replace destroyed phloem and bark, and even to form adventitious roots. Such trees die only if weed competition becomes too great, or if termites follow the burrows and eat away the remaining wood.

Trees a year or two old are nearly always killed if attacked by borer, and the insect dies also since the plants are not large enough to contain it. Trees three or four years old suffer severely, become yellow and the crop fails to mature, but at this age are old enough to regenerate.

Unfortunately, farmers frequently fail to appreciate how seriously their coffee is damaged by borer. As already indicated most borers live at or below ground-level, so that trees which showed little damage are frequently seriously riddled in the bole and root system. It is not until the trees are uprooted that an accurate appraisal can be made.

Host-plants.

Morstatt (1912) concluded that, as coffee trees growing near natural forests were the first to be infested, *A. leuconotus* must live naturally in the forest, but as he was unable to find any wild hosts it was apparent that the insect was only sparsely distributed. Ritchie found five species of wild trees carrying borer (Davies, 1937), viz.: *Oxyanthus speciosus* (Mrali), *Randia* sp. (Mbuchi), *Vangueria* sp. (Mroo), *Pavetta oliveriana* (Kifufu), *Rytigynia schumanii* (Mroo mdogo). *Randia* and *Vangueria* are common and can nearly always be found carrying the borer.

Smee (1936) reported that *Erythroxyton emarginatus* was a wild host in Nyasaland, and Knight reported *Gardenia urcelliformis* as a host in Kenya, and suspected that *Vangueria linearisepala* and *Canthium* sp. were also hosts.

Coffea arabica, *C. liberica*, *C. eugenioides* and *Lachnastoma khasiana* are the only known species of coffee to be affected by the borer. It appears that *C. canephora* (Robusta) can be attacked, but shows a peculiar form of resistance. Where beetles were introduced to cages surrounding the stem of *arabica* grafted on a *robusta* root-stock, approximately equal numbers of eggs were laid in the scion and stock. Those eggs in the *arabica* scion hatched normally and proceeded to ring-bark the tree. Most of the larvae were removed to prevent excessive damage, but a few were allowed to enter the wood, where they were unfortunately destroyed in error. In the root-stock the bark split and curled soon after oviposition at each egg site thus exposing the eggs. None of the eggs distributed over four root-stocks ever gave rise to a ring-barking larva. A further interesting point was that none of the larvae in the scions attempted to enter the stocks, although they might have been expected to do so since the unions were near ground-level.

Control measures.

Historical review.

Gooch (1874) devised a means whereby borer populations could be held in check and his recommendations, with few modifications, have served for 80 years. He recommended that (1) the stem of the tree be rubbed to expose ring-barking larvae in their surface burrows, (2) wood-boring larvae be removed with a wire, (3) adult beetles be collected in the flying season and (4) all badly infested trees be uprooted and burnt. Warburg, in 1895, recommended the use of carbon bisulphide as a fumigant in the burrows to kill wood-boring larvae and various other suggestions along the same line of approach have been put forward since. Smee (1927) recommended paradichlorobenzene crystals; Robertson (1949) recommended a mixture of ethylene dichloride and carbon tetrachloride, and Fiedler (1950) suggested the use of Xylamon (a preparation the basis of which is a liquid chlornaphthalene (*Rev. appl. Ent.*, A 25 pp. 658-659, 1937)).

These measures, if applied vigorously, kept the borer under control as Davies (1937) testifies, but if an infestation was allowed to get out of hand it was costly and difficult to bring it under control again. Fumigants work well, but unfortunately the burrows have to be found first, and these in nearly 80 per cent. of the cases begin underground and are difficult to detect. Such measures were put to test in 1953 to obtain an estimate of their efficiency against wood-boring larvae. A team of African assistants, well versed in borer control, were given two sets of 50 trees to examine for wood-boring larvae. In the first 50 trees, after careful examination, only 10 larvae of the borer were detected, but when the trees were uprooted and cut up a further 18 were found. In the second 50 trees, 38 borer larvae were detected after a particularly careful examination, but another 46 were found later when the trees were dissected. It is apparent, therefore, that if an experienced team can destroy less than half of the population

of wood-boring larvae if given time to make a careful inspection, the farmer, whether peasant or estate owner, can hardly be expected to do much better.

Various other measures have been tried over the years. The use of tar (Mayné, 1923), California Bouillie and other repellents (Knight, 1939) were tried with no success. Ritchie (1933) suggested that metal shields, roofing felt, bordeaux paste or a lime-sulphur paste might be used to protect the tree, but Moffat & Allan (1934) reported that repellents and barriers were not satisfactory. Mayné (1923) and Notley (1951) tried applying paris green and lime to the main stem, and Smee (1927) experimented with lead arsenate, sodium fluoride and zinc sulphate using rosin and washing soda as stickers, but with no success. Spraying the trees with paris green at the time of a beetle outbreak (Notley & Tapley, 1951) gave only a limited measure of success and was not further pursued.

An extensive campaign against wild host trees in the coffee lands of Kilimanjaro and Meru in the 1930's resulted in the destruction of an estimated two million trees (Davies, 1937). The success of the scheme has not been measured, but it was reported that only about six larvae were found per hundred trees. In spite of the campaign, wild hosts are still apparent in coffee-growing areas, and many of them harbour the pest. Some attempt was later made to destroy wild hosts with arboricides, but with little success. Finally it was concluded that the population of coffee borer in wild host trees was infinitesimal compared with populations in coffee trees, and did not justify further attention. With the arrival of dieldrin, which has made possible the satisfactory control of *Anthores* populations, the question of wild host trees lost its importance.

Recent work at Lyamungu.

Investigations into the control of *A. leuconotus* with the help of newly discovered insecticides began when Notley (1951) found that painting the stem with DDT gave no useful control of borer. In 1950, parathion and schradan were found not to have any effect on ring-barking or wood-boring larvae (Tapley, 1952). An experiment using stickers with massive doses of BHC, DDT, toxaphene and dieldrin on the stems of coffee trees in 1951 failed because no beetles appeared in the experimental plot, but dieldrin, DDT and BHC (in that order of toxicity) still persisted on the bark in sufficient quantities to kill *Antestiopsis lineaticollis* (Stål) (PENTATOMIDAE) in test cages, even 126 days after application, during which 40 inches of rain fell. DDT and dieldrin were also found to kill beetles (Tapley, 1953). BHC was excluded from later trials since it was suspected of imparting a taint to coffee liquor, but emulsified solutions of DDT and dieldrin with stickers were found effective in keeping treated stems significantly free of new infestations. An emulsified solution of dieldrin (with stickers) applied to the stem appeared to be about four times more effective than DDT against the female beetles, but the results could not be analysed (Tapley, 1954a). These figures were confirmed during investigations in 1953, and moreover it was found that the insecticide on the stem was killing not only adult beetles, but also ring-barking larvae, presumably because some of the insecticide had penetrated into the bark (Tapley, 1954b). It also became apparent that quite large doses of insecticide, even though they eventually killed the females, could not prevent them from laying eggs before dying. The use of stickers in association with insecticides was questioned, and Robinson & Mesmer (1957) began investigations into DDT deposits on coffee stems with and without stickers. The observations showed that DDT was lost rapidly during the first few weeks and later very slowly. A regression of the log DDT content of bark against log time showed the loss to be linear. A regression of resin with the DDT against time showed a significant deviation from linearity, and it appears the loss was somewhat slower.

However, as DDT persisted well without stickers, and as it was feared that resins may affect DDT biologically by masking the insecticide, they were not used again.

Dimefox (as Hanane) applied to the soil was not found to have any effect on ring-barking larvae (Tapley, 1954b).

By 1954 (Tapley, 1955a) the last of a long series of small experiments (not all reported) was completed. It was known that if an emulsified solution of dieldrin without stickers was painted or sprayed heavily on coffee stems a good measure of protection could be obtained. Also during the year the use of insecticide lacquers was tested and found very satisfactory in small-scale trials (Tapley, 1955b). Foster (1955) studied the effects of DDT, dieldrin, endrin and chlordane on the beetles in the laboratory and concluded that dieldrin and endrin were considerably more toxic than chlordane and DDT. As dieldrin and endrin were similar in toxicity it was decided to use dieldrin exclusively in later trials.

The 1954/55 '150 acre' trial.

A large field-scale trial was needed to prove finally that the application of dieldrin to the stems was fully effective in protecting the tree, to measure the optimum dose of insecticide and to find out for what period the insecticide persisted in effective concentration. The work has already been very briefly reported (Tapley, 1956, 1958b). Mr. P. R. Robinson, Statistician to E.A.A.F.R.O., advised on the design of the experiment. A 6 × 2 randomised block was replicated on 14 estates in the Moshi and Arusha districts, one replicate being placed on each estate where the coffee borer was known to be present in large numbers and causing extensive damage.

Treatments were as follows:—

- A — Check-plots.
- B — 0.50% dieldrin, in emulsified solution, sprayed on the lower 18 in. of main stem.
- C — 0.75% " " " " " " " " " " " "
- D — 1.00% " " " " " " " " " " " "
- E — 1.50% " " " " " " " " " " " "
- F — 10% dieldrin contained in urea and alkyd resins.

I—one application of insecticide: before the 'short' rains.

II—two applications of insecticide: before 'short' rains and again before the 'long' rains.

Each plot contained 22 × 22 trees planted at 9-ft. intervals and the whole experiment covered over 150 acres. The plots were usually randomised in a line along roads for ease of accessibility.

The emulsified solution of dieldrin made from 'Dieldrex 15' was coloured with methylene blue at the rate of 1 oz. of methylene blue to 10 gallons of emulsified solution. The blue dye served as a marker to enable the operator and supervisor to check the quality of spraying, and to indicate the presence of the rather toxic chemical on skin and clothing. The emulsified solutions were sprayed on the lower 18 in. of stem of each coffee tree in the respective plots with pressure-retaining knapsack sprayers fitted with trigger taps, and ceramic Bray fan jets, size 00. The average amount of spray applied per acre of 540 trees (9 ft. × 9 ft. spacing) was 18.75 gal., with a maximum of 24 gal., and a minimum of 14 gal. per acre on individual plots.

The 10 per cent. dieldrin in urea and alkyd resins was sprayed with portable paint-spraying apparatus at the rate of 5 to 6 pints per acre of 540 trees, covering the same amount of stem as the treatments with emulsified solution.

The first application of treatments, in November and early December 1954, was timed to precede the emergence of beetles with the short rains. The second treatment, in March 1955, where applied, preceded the heavy rains and the

second beetle emergence of the season. However, in the Arusha district the second application of insecticide was not made as dissection of trees uprooted in this area indicated that a second big emergence of beetles could not be expected during the long rains, and accordingly that a further application would have been wasted.

In assessing the results of treatments, the outer four rows of each plot were regarded as guard trees which were not examined, leaving a plot of 14 × 14 trees for examination. To detect new borer damage, each tree was examined by experienced personnel under constant supervision. It was found that one man could satisfactorily examine only 12 to 15 trees per hour. Check-plots were first examined, and if no borer could be detected, the remaining plots were not examined. However, if new borers were found in the check-plots, at least some of the treated plots were examined.

The timing of assessment was carefully made so that most larvae were reaching the end of the ring-barking phase and could therefore be more easily detected. Where a new burrow in the bark was found to enter the root system, or if the insect had entered the wood, it was counted as being alive since it had safely reached an untreated section. However, in most cases the insects were actually found, removed, and taken to the laboratory.

Results.—These are shown in Table II. The most outstanding observation was that the over-all new borer population following the treatment was practically eliminated in the treated plots, and was very much less than expected in the check-plots. The total number of new living and dead larvae in the 28 check-plots in the first assessment was only 383, and in the second assessment 372. The number expected, judging from previous experience of the farms, was at least 2,000, and it would not have been surprising if it had been 4,000 or 5,000. There was no indication that the over-all borer population was less in the untreated parts of the estates, so that the reduction must be ascribed to the treatment, and not to mere coincidence.

It has been suggested that the treatment, either the insecticide or the methylene blue, might have acted as a repellent, and so reduced the over-all population of beetles. However, there was no evidence to support this view: female beetles had already been observed to lay eggs in stems heavily treated with dieldrin and showed no tendency to avoid the insecticide. In a subsequent field experiment it was shown that beetles laid as readily in stems treated with methylene blue (unaccompanied by insecticide) as they did in untreated stems.

In only five estates, numbers 1, 3, 5, 7 and 14, where the borer populations were known to be exceptionally high (estimated at over 2,000 per acre of coffee), did the check-plots show a considerable number of living larvae, compared with the treated plots which showed no signs of a new infestation.

It was safe to conclude, without statistical analysis, that all treatments were effective, and that the use of 0.5 per cent. dieldrin in emulsified solution, the cheapest treatment, was completely satisfactory. It was possible, however, that the optimum rate of insecticide had not been found and might well have been less.

Although only the lower 18 in. of stems (the only parts sprayed) were examined in the assessment, mainly because there was no time to examine the whole stem, which is usually 5 ft. tall, it was noticed that ring-barking larvae were sometimes working above the treated zone. While no numerical data are available, it can be stated that the numbers were few. This was more or less as expected, but it was also expected that if a large area of coffee was treated, the over-all population of coffee borer would, in time, be so reduced that very few would remain in the tops of the trees. Experience has shown that this is so, and that the residual number living in the upper reaches of the stem forms only a very minute fraction of the previous population. Farmers' reports in 1958 and 1959

TABLE II.
Results of 150-acre randomised-block experiment.
Number of coffee-borer larvae found in plots treated with dieldrin or untreated.
(Number alive to left of each column, number dead to right.)

Replicate and district of location	Intended number of applications	1st assessment : March/April 1955						2nd assessment : Sept. 1955 or later					
		Treatment						Treatment					
		A	B	C	D	E	F	A	B	C	D	E	F
1 Moshi	I II	23 X	5 0 X	5 0 X	6 0 X	3 0 X	6 NT NT	5 2 0	0 0 2	X X	X X	X X	0 0 0
2 Moshi	I II	0 0 0	0 0 0	X X X	X X X	X X X	NT X	0 0 0	X X	X X	X X	X X	X X
3 Moshi	I II	0 0 0	0 0 0	X X X	X X X	X X X	X NT	2 17 2	0 0 0	X X	X X	X X	1 1 0
4 Moshi	I II	2 3	1 0 0	0 0 4	X 0 0	X 0 1	X 0 4	8 6 0	0 0 1	X X	X X	X X	0 0 2
5 Moshi	I II	71 X	59 1 X	42 0 X	47 0 X	70 0 44	NT X	3 10 1	0 0 1	X X	X X	X X	1 0 0
6 Moshi	I II	4 X	4 0 0	0 0 X	1 0 X	0 0 X	0 NT	0 0 0	0 0 0	X X	X X	X X	X X
7 Moshi	I II	58 13	26 6	0 0 3	5 0 X	6 2 X	31 0 8	62 30 8	14 4 0	X X	X X	X X	1 4 69

TABLE II.—continued.

Replicate and district of location	Intended number of applications	1st assessment: March/April 1955						2nd assessment: Sept. 1955 or later					
		Treatment						Treatment					
		A	B	C	D	E	F	A	B	C	D	E	F
8 Arusha	I II	4 7	2 0	0 0	0 0	0 1	NT 0	0 4	X 0	X X	X X	X X	NT 0
9 Arusha	I II	1 0	3 0	0 X	0 X	0 X	0 NT	0 0	X X	X X	X X	X X	X NT
10 Arusha	I II	0 0	0 0	0 X	X X	X X	X NT	0 0	X X	X X	X X	X X	X NT
11 Arusha	I II	5 5	1 0	0 0	0 0	0 0	NT 0	0 0	X X	X X	X X	X X	NT X
12 Arusha	I II	0 0	0 0	0 0	X X	X X	X NT	0 0	X X	X X	X X	X X	X NT
13 Arusha	I II	0 2	0 0	0 0	X 0	X 1	NT 1	0 0	X X	X X	X X	X X	NT X
14 Arusha	I II	26 45	4 1	0 1	5 27	0 4	X 0	94 52	2 0	1 18	X X	X X	19 7

NT = Treatment not applied.
X = Not examined.

A: Check-plots.

B: 0.5% dieldrin.

C: 0.75% dieldrin.

D: 1.0% dieldrin.

E: 1.5% dieldrin.

F: dieldrin lacquer.

I = one application of insecticide (November/December 1954).

II = two applications of insecticide, November/December 1954 and March 1955 (second application not made in Arusha district).

Treatment F comprising a single application only.

indicated that at the most, two or three borers per acre survive in this way, and many other farmers reported that *A. leuconotus* has virtually been eliminated from their coffee.

Persistence of dieldrin.—At the end of the first year, most of the plots were abandoned and the experimental areas were re-treated in the routine farm applications. A few plots were uprooted. In estates numbers 7 and 14, however, the experimental plots and surrounding coffee remained untreated. Two and a quarter years following the original treatment the plots were re-examined.

Of 460 trees examined in the three 'B' plots (0.5 per cent. dieldrin, single application) six ring-barking larvae only could be detected, but in 334 trees in the check-plots, 208 ring-barking larvae were found. In the dieldrin plots, many dead larvae were noted in the treated parts of the stem, but above the treated area living larvae were found in appreciable numbers. The details have been reported more fully elsewhere (Tapley, 1958b).

It is apparent, therefore, that a single application of dieldrin can give coffee trees a good measure of protection against *A. leuconotus* for well over two years.

The chemical persistence of DDT and dieldrin in coffee bark has been studied by Robinson & Mesmer and the details of DDT persistence have been published (1957). From data supplied by Robinson & Mesmer (unpublished) it appears that a mean initial deposit of dieldrin at 230 mg. per sq. ft. is reduced to 107 mg. per sq. ft. one month after application, and 85 mg. per sq. ft. two months after application. It is evident that dieldrin is lost more quickly from coffee bark than is DDT, as is the case on coffee leaves (K. C. Sleep, *Misc. Rep. Colon. Pest. Res. Unit Arusha* no. 204, 1958). It is believed that the initial deposit of dieldrin in coffee stems following an application of an emulsified solution, containing 0.5 per cent. dieldrin, at approximately 19 gal. per acre is from 300 to 400 mg. per sq. ft. Residues of dieldrin in samples taken from these treated trees some 27 months after application were found by Dr. Sleep to be 9 mg. per sq. ft. of bark.

Thus, although the initial loss of dieldrin may be high, about 50 per cent. in the first month, the loss later slows down very considerably, as with DDT. It seems unlikely that much of the insecticide is contained at the surface of the bark, but may be concentrated in the bark fissures which reach the living tissue of the phloem. As Robinson & Mesmer suggest (1957), a concentration of insecticide near the living tissue where ring-barking larvae operate may be effectively placed. It seems certain that the long residual action of dieldrin in coffee bark is not due so much to the insecticide having effect on the beetles, but to a concentration of insecticide contained in the bark fissures affecting ring-barking larvae.

On the other hand, a high initial deposit of dieldrin is known to kill the female beetles, while ovipositing for a period of 6 weeks and after 16.8 in. rain (Tapley, 1954a). It is also believed that emerging beetles can pick up a lethal dose of insecticide from the bark, since beetles have been observed dead in the pupal chamber apparently after attempting to emerge. Heavily infested trees were uprooted, treated with dieldrin and placed in an insect-proof room. The room was examined daily for emergent beetles; such as were found were moribund or dead. However, it was impossible to be sure whether the beetles picked up a lethal dose of insecticide while actually emerging, or subsequently from walking on treated bark. The matter was not pursued further.

On the whole it would seem that the effect of the residual insecticide in the bark on ring-barking larvae was the most important factor in controlling the pest.

Dieldrin lacquer afforded the trees a good measure of protection, but at the twenty-seventh month there were signs that the control was failing and was less effective than the treatment with emulsified solution. For this reason, and as the lacquer is expensive to apply, its use was abandoned.

Comments on the design of the experiment.

The 150-acre experiment was designed to deal with two populations, the beetles which are mobile, and ring-barking larvae which are static. First, it was assumed that the beetles were slow in moving about in coffee and that a single female would confine its oviposition to groups of about 25 trees. Hence beetles were expected in general to remain in plots in which they settled to oviposit, and that the guard rows of each plot would prevent a beetle migrating into a plot and laying eggs in the assessed trees before dying. However, this surmise was found to be completely wrong. Beetles appeared to be far more mobile than was expected, and the insecticide in the treated plots had the effect of reducing populations in that general area to such an extent that even in untreated plots not enough beetles remained to reinfest the trees to an appreciable extent.

Secondly, it was assumed that females would succeed in laying some eggs in treated plots before being overcome by the treatments. This assumption also appears to have been wrong for the most part, and in fact very few eggs were laid. This also might be attributed in part to the over-all reduction of beetle numbers.

It would appear, therefore, that it is necessary to separate the effects of the treatment on the two populations as far as is possible.

To test the effect of the insecticide on the adults it might have been better to have had the plots widely scattered over the estate in such a way that the treated areas could not have reduced the over-all adult population. However, no opportunity arose to test this theory.

Other experiments and observations: 1954 and 1955.

At the same time as the main experiment was in progress a number of small African-owned plots were treated, and here the insecticide was applied with paint brushes. A method was evolved whereby the roots could be protected from borer at a very low cost, allowing for manual control methods to be applied above ground. The details of the method were published in a Coffee Board pamphlet (Tapley, 1955c, Swahili version), but it never became popular and African farmers later adopted the practice of brushing the lower 18 in. of stem with the insecticide.

Also during 1954 and 1955 a number of farmers, mostly using paint brushes, used dieldrin at concentrations ranging from 0.5 per cent. upwards and in each case it was found that the trees had not been reinfested. The only borers that could be detected were in their final instars and were presumed to have entered the wood before the trees were treated.

The recommendations to farmers.

The final recommendations issued to coffee farmers in Tanganyika (Tapley, 1957) were as follows:—

- (1) Use an emulsified solution containing 0.5 per cent. dieldrin to which has been added methylene blue at the rate of 1 oz. per 10 gal. water.
- (2) Apply at the rate of 18 gal. per acre; treat the lower 18 in. of stem using either sprayers or paint brushes.
- (3) Apply the insecticide preferably in November.
- (4) Trees should be treated once each year for the first two years, and thereafter every second year.
- (5) Young coffee trees should be re-treated annually until the main stem reaches full size.

The cost: about 40s. per application.

These recommendations have been accepted and the results have been very satisfactory. *A. leuconotus* can no longer be regarded a pest of economic

importance and it is considered that coffee-growing can now be extended in the lower areas (Soper, 1958, p. 6) where previously intense borer infestation was a limiting factor. In Kenya also, dieldrin banding has been effective in completely eliminating borer (McCrae, 1959).

Summary.

Anthores leuconotus Pasc., indigenous in East, South-East, South and South-West Africa, is an important ring-barking and wood-boring pest of the main stem and root of *arabica* coffee. The duration of the life-cycle ranges from 12 to 25 months, with most individuals requiring 16–20 months. Thus beetles developed from eggs laid during the long rains (April–June) of one year will mostly emerge during the short rains (Nov.–Jan.) of the following year, with some appearing during the rains preceding and others during the ensuing rains.

If the mean life-cycle is taken to be 18 months, the approximate duration of each stage is as follows:— eggs require 21–23 days for eclosion; larvae in the first five instars ring-bark the tree for 4 months, and those in the final two instars bore into the wood for 12 months; the pupal period lasts about $4\frac{1}{2}$ weeks, and the beetle remains in the tree for a further two weeks before emerging.

Oviposition, which takes place mainly in the hours of darkness from sundown to midnight, is described.

The growth rate of the larvae was found to be much higher while the larvae were feeding on soft tissues (*i.e.*, ring-barking) than while feeding on hard tissues (wood-boring). The mean weekly increase of the head capsule of the ring-barking larva was 0.12 mm., and of the wood-boring larvae, 0.033 mm.

A method of observing living wood-boring larvae in their burrows is described.

Female pupae, with a mean weight of 1.23 g., were significantly heavier than male pupae with a mean of 0.99 g. Male and female beetles were found in approximately equal numbers in the field, but males emerged from the trees slightly earlier than the females.

Where coffee is infested with borer it was noted that in the warmer, lower elevations the larvae mostly live in the base of the stem and main root system, but at higher, colder elevations, and also in heavy shade, more live well above ground-level.

Larval mortality appears to be high, perhaps as much as 75 per cent. One species of egg-parasite was found, and it is believed that five species of Hymenopterous parasites attack ring-barking larvae, and four species attack the wood-borers.

Loss of crop due to borer in one case where infestation was very light and not continuous was estimated at 0.4 cwt. of clean coffee per acre per year. Where infestations are heavy and continuous, the loss is certainly very much higher.

Wild host trees are listed and their importance discussed. If Robusta coffee is attacked the trees show a form of resistance; the bark splits open following oviposition and eggs are left exposed.

Control measures recommended to coffee growers in the past have been reviewed and found to be unsuitable for modern farming. Experiments in which the effectiveness of various insecticides and methods of application were tested since 1950 are described.

A spray containing 0.5 per cent. dieldrin in emulsified solution applied at the rate of 18 gal. per acre to the lower part of the coffee stems (540 trees per acre) has given excellent protection from borer and persists effectively in the bark for up to 27 months. A marker, methylene blue, is included in the spray mixture to warn operators of the presence of dieldrin on skin and clothing and to improve spraying efficiency. The persistence of dieldrin and its method of destroying borer is discussed.

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Finally, I am most grateful to the many coffee farmers on estates and small-holdings who permitted their coffee to be used in field trials and trees to be destroyed for collection of the results.

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References.

- ANDERSON, T. J. (1928). Annual report of the Entomologist (Kenya Colony) 1927. —*Rep. Dep. Agric. Kenya* 1927 pp. 208–219.
- CHEVALIER, A. (1947). Les caféiers du globe. Fascicule III.—*Encycl. biol.* **28**, 356 pp. Paris, Lechevalier.
- 356 DAVIES, R. M. (1937). The control of white stem borer of coffee.—*E. Afr. agric. J.* **2** pp. 293–297.
- DUFFY, E. A. J. (1946). A contribution towards the biology of *Prionus coriarius* L. (Coleoptera, Cerambycidae).—*Trans. R. ent. Soc. Lond.* **97** pp. 419–442.
- DUFFY, E. A. J. (1957). A monograph of the immature stages of African timber beetles (Cerambycidae).—338 pp. London, Brit. Mus. (nat. Hist.).
- 258 FIEDLER, O. G. H. (1950). Entomologisches aus Afrika. (Beobachtungen über Kaffeeschädlinge).—*Z. angew. Ent.* **32** pp. 289–306.
- FOSTER, R. (1955). Laboratory observations on the effects of insecticides on the white coffee borer beetle.—*E. Afr. agric. J.* **21** pp. 6–9.
- FULLER, C. (1901). First report of the Government Entomologist (Natal Dep. Agric.) 1899–1900.—150 pp.
- GARDNER, J. C. M. (1934). On some Coleopterous larvae from Uganda.—*Bull. ent. Res.* **25** pp. 149–154.
- GOOCH, W. D. (1874). [Habits of the longicorn “coffee-borer of Natal.”]—*Proc. ent. Soc. Lond.* **1874** pp. xiv–xvi.
- JAMES, H. C. (1928). Progress report on insect pests.—*Bull. Dep. Agric. Kenya* no. 22, 9 pp.
- KNIGHT, C. D. (1939). Observations on the life-history and control of the white borer of coffee in Kenya.—*E. Afr. agric. J.* **5** pp. 61–67.
- 2 LEPESME, P. & VILLIERS, A. (1944). Les longicornes du caféier en Afrique intertropicale.—*Trav. Sect. tech. Agric. trop.* Sér. 1 pp. 27–70.
- LEWIN, C. J. (1936). Northern Rhodesia. Department of Agriculture. Annual report for the year 1935.—23 pp.

- McCRAE, D. J. (1959). Report of the Entomologist.—*Rep. Coff. Res. Sta. Kenya* 1957–58 pp. 68–70.
- MAYNÉ, R. (1923). Principaux ennemis des caféiers au Congo Belge.—*Ann. Gembloux* **29** pp. 377–384.
- MOFFAT, U. J. & ALLAN, W. (1934). A preliminary note on the white borer of coffee at Abercorn.—*Ann. Bull. Dep. Agric. N. Rhod.* 1933 pp. 39–41.
- MORSTATT, H. (1912). Die Schädlinge und Krankheiten des Kaffeebaumes in Ostafrika.—*Pflanzer* **8** Beih. 2, 87 pp.
- MORSTATT, H. (1935). Kaffee-Schädlinge und -Krankheiten Afrikas. I. Kaffeebohrer (Stammböhrer).—*Tropenpflanzer* **38** pp. 413–431.
- NOTLEY, F. B. (1951). Annual report of the Entomologist, Lyamungu, for 1949.—*Rep. Dep. Agric. Tanganyika* 1949 pp. 116–117.
- NOTLEY, F. B. & TAPLEY, R. G. (1951). A note on white borer of coffee.—*E. Afr. agric. J.* **16** p. 130.
- PASCOE, F. P. (1869). Descriptions of some new species of Lamiidae.—*Ann. Mag. nat. Hist.* (4) **4** pp. 203–211.
- RITCHIE, A. H. (1933). Report of the Entomologist, 1932.—*Rep. Dep. Agric. Tanganyika* 1932 pp. 68–72.
- ROBERTSON, J. K. (1949). The control of white stem-borer (*Anthores leuconotus*) in arabica coffee.—*E. Afr. agric. J.* **15** pp. 35–37.
- ROBINSON, J. & MESMER, E. T. (1957). The persistence of insecticides deposits applied to bark of coffee trees (*Coffea arabica*). I. DDT deposits.—*E. Afr. agric. J.* **23** pp. 130–134.
- SMEE, C. (1927). Report of the Entomologist.—*Rep. Dep. Agric. Nyasaland* 1926 pp. 13–20.
- SMEE, C. (1936). Report of the Entomologist.—*Rep. Dep. Agric. Nyasaland* 1935 pp. 23–25.
- SOPER, J. R. P. (1958). Annual report of the Department of Agriculture, Tanganyika, 1957. Part I.—43 pp.
- TAPLEY, R. G. (1952). Annual report of the Entomologist, Lyamungu, for the year 1950.—*Rep. Dep. Agric. Tanganyika* 1950 pp. 173–175.
- TAPLEY, R. G. (1953). Annual report of the Entomologist, Lyamungu, for 1951.—*Rep. Dep. Agric. Tanganyika* 1951 (Rep. tech. spec. Offrs) pp. 49–52.
- TAPLEY, R. G. (1954a). Annual report of the Entomologist, Lyamungu for 1952.—*Rep. Dep. Agric. Tanganyika* 1952 pt. III pp. 43–49.
- TAPLEY, R. G. (1954b). Annual report of the Entomologist, Lyamungu, for the year 1953.—*Rep. Dep. Agric. Tanganyika* 1953 pt. II pp. 60–65.
- TAPLEY, R. G. (1955a). Annual report of the Entomologist, Lyamungu, for the year 1954.—*Rep. Dep. Agric. Tanganyika* 1954 pt. II pp. 62–69.
- TAPLEY, R. G. (1955b). Insecticidal lacquers and white coffee-borer control.—*E. Afr. agric. J.* **20** pp. 145–148.
- TAPLEY, R. G. (1955c). The white coffee-borer and how to fight it. [In English & Swahili.]—[9] pp. Lyamungu [Tanganyika Coff. Bd].
- TAPLEY, R. G. (1956). Annual report of the Entomologist, Lyamungu, for the year 1955.—*Rep. Dep. Agric. Tanganyika* 1955 pt. II pp. 43–46.

- TAPLEY, R. G. (1957). The white coffee-borer and how to fight it. Supplement. —[In English & Swahili.] [2] pp. Lyamungu [Tanganyika Coff. Bd].
- TAPLEY, R. G. (1958a). Entomology, Lyamungu.—*Rep. Dep. Agric. Tanganyika* 1956 pt. II pp. 92-93.
- 141 TAPLEY, R. G. (1958b). Lyamungu, Entomology.—*Rep. Dep. Agric. Tanganyika* 1957 pt. II pp. 75-78.
- WARBURG, O. (1895). Ein neuer Kaffeeschädling aus Afrika.—*Mitt. dtsh. Schutzgeb.* 8 pp. 130-140.



FIG. 1. Ring-barking damage and entrance to a wood burrow. The bark of the superficial burrow has been removed to show the extensive damage caused by a single larva.



FIG. 2. A dissected burrow in coffee wood covered with 'perspex' for observation of larval tunnelling.

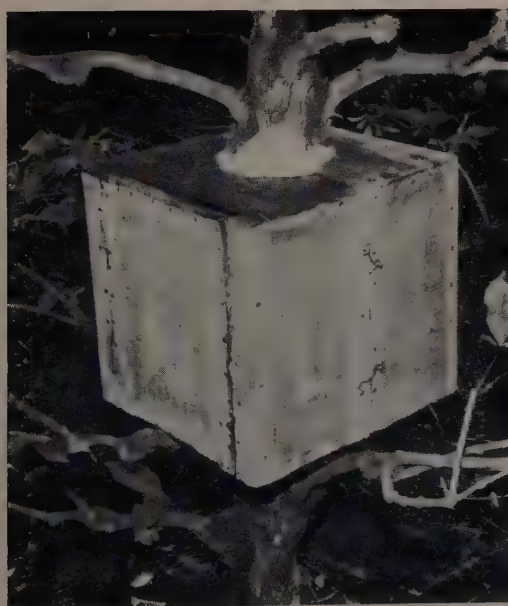


FIG. 3. A cage used to contain beetles on a stem in order to obtain eggs and larvae of a known age.



FIG. 4. A larval burrow, showing the entrance below a lateral root, the burrow tightly filled with frass, the pupal chamber and the emergence hole at its upper end.

THE BEHAVIOUR AND SPECIFICITY OF *MONOCTONUS PALUDUM*
MARSHALL* (HYM., BRACONIDAE), A PARASITE OF *NASONOVIA*
RIBIS-NIGRI (MOSLEY) ON LETTUCE.

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(PLATES X & XI.)

The Braconid subfamily APHIDIINAE is confined in its host relations to aphids, but there exists, within the APHIDIINAE, considerable variation in the number of aphid species which a given parasite can successfully attack. The most recent host/parasite record for aphids is that of Thompson (1950), but this is by no means comprehensive and, although several studies on bionomics of the parasites have been carried out, experimental work upon the host preferences within the APHIDIINAE themselves appears to have been largely neglected. Ulyett (1938) stressed the fact that a great deal of work was required to be done before the question of specific relations could be placed on a sound basis.

The present study was undertaken with the objects of gaining information on the problem of host/parasite relations; to determine which of the factors, host finding, host selection or host suitability, is responsible for the success or failure of parasitism in the species under consideration; to make a contribution to the host/parasite records, and to develop techniques for further research into this type of problem.

Collection of material.

The aphids and parasites were collected from lettuce plants grown in the Knighton district of Leicester during 1953-54, and in the Newcastle upon Tyne district during 1958. 'Sessile' aphids, i.e., shiny and bloated aphids containing parasite pupae, were removed from the plants, together with a small piece of leaf to which they adhered, and were placed separately in specimen tubes to await emergence of the adult parasites.

The parasites and hyperparasites of lettuce aphids which were collected in this way are listed in Table I.

Monoctonus paludum was the parasite which occurred in greatest numbers, and for that reason this species was selected for detailed study. The male and female of *M. paludum* are shown in figs. 1 and 2, respectively, and a description of them is given, under *M. crepidis* (Hal.), by Stary (1959).

Observations.

It can be seen from Table I that, within the complex of lettuce aphids in the field, *M. paludum* is restricted to *Nasonovia ribis-nigri*. Laboratory observations on the oviposition behaviour of the parasite were then carried out in order

* Stary (1959) in a revision of the genus *Monoctonus* Haliday identifies *M. paludum* Marshall with *M. crepidis* (Hal.) which has been recorded from other aphid hosts on plants related to lettuce.

The term "non-lettuce aphids" in the text of the present paper refers to species of aphids which have been taken from plants unrelated to lettuce.

† Part of the work included in this paper was carried out with a research grant at Leicester University and was presented as an M.Sc. thesis at Sheffield, 1955.

to determine why other species of lettuce aphids did not act as hosts for this parasite.

Typical oviposition behaviour.

When a female of *M. paludum* is attacking a suitable individual of *N. ribis-nigri* the parasite approaches the aphid, examines it with the antennae, reaches forward to grasp it with the forelegs, and, with a swift motion, bends its abdomen forward and under, in the manner described by various authors for other species of Aphidiine parasites. With a forward thrust it inserts its ovipositor into the ventral surface of the aphid in the transverse suture between the first and

TABLE I.

Parasite or hyperparasite	Aphid host
BRACONIDAE	
APHIDIINAE	
<i>Monoctonus paludum</i> Marshall	<i>Nasonovia ribis-nigri</i> (Mosley)
<i>Aphidius ribis</i> Hal.	<i>Nasonovia ribis-nigri</i> (Mosley)
<i>Aphidius matricariae</i> Hal.	<i>Nasonovia ribis-nigri</i> (Mosley)
	<i>Myzus persicae</i> (Sulz.)
	<i>Aulacorthum solani</i> (Kalt.)
<i>Aphidius</i> spp.	<i>Hyperomyzus lactucae</i> (L.)
<i>Aphidius avenae</i> Hal.	<i>Macrosiphum euphorbiae</i> (Thos.)
CHARIPINAE	
<i>Charips</i> sp.? <i>tscheki</i> (Giraud)	<i>Myzus persicae</i> (Sulz.)
APHELINIDAE	
<i>Aphelinus asychis</i> Wlk.	<i>Nasonovia ribis-nigri</i> (Mosley)
	<i>Aulacorthum solani</i> (Kalt.)
	<i>Macrosiphum euphorbiae</i> (Thos.)

second pairs of legs. In this position the parasite and aphid remain motionless for a period of 13-20 seconds, the parasite with its wings extended behind it, all the while retaining its hold on the aphid with its forelegs and standing antero-lateral to the host. It then withdraws its ovipositor until it is a fraction away from the aphid's body, pauses in this position for a few moments, straightens its abdomen and finally releases the aphid. The site for oviposition is usually very precise, and, should the parasite first contact the aphid from behind, it swings around rapidly into a position from which it can insert its ovipositor anteriorly into the site described. Later observations proved that the deposition of an egg in any other place was of rare occurrence, and was only observed when the parasite was attacking large, active aphids.

Having attacked an aphid, the parasite may remain in one place for some time stroking the posterior end of its abdomen with its hind legs, as though in an attempt to clean it, and flexing it at intervals. It also strokes its antennae between its forelegs and mouth parts, and, under the binocular microscope, it can be seen to be ridding itself of a scaly deposit which has collected on its body. When these preening operations are completed the search for more aphids is renewed, and, provided that further suitable aphids can be found, the sequence of events may be repeated many times in succession.

When the parasite is presented with a variety of aphids, particularly if these are from different plants, then not all the aphids which it encounters will be attacked. Some are merely examined by means of the antennae for a brief or

for a more prolonged period, whilst with others the parasite follows this examination by inserting its ovipositor. This insertion may, however, be brief and the ovipositor may be withdrawn again before sufficient time has elapsed for the deposition of an egg.



Fig. 1.—Male of *Monoctonus paludum* Marshall.



Fig. 2.—Female of *Monoctonus paludum* Marshall.

Very large aphids are often able to struggle free from the parasite, and very small aphids are difficult to attack in that they are carried off the substratum, impaled upon the parasite's ovipositor, and are subsequently difficult for the parasite to dislodge.

Conditions for observations.

Preliminary observations were carried out to determine the conditions most suitable for recording host selection and oviposition behaviour, and as a result of these, the following precautions were applied in all subsequent observations.

(a) *Fertilised female parasites, approximately one-day old, which had emerged from large hosts, and which had recently been fed on honey were used in each case.*—It was found that freshly emerged parasites would not oviposit for some hours, and so the usual practice was to induce the parasites to mate as soon as possible after emergence, and to use them for the observations on the following day. The recent work of Edwards (1954) confirms the importance of carefully controlling the age, size and condition of parasites in behaviour experiments of this type.

(b) *Precautions were taken to ensure that only unparasitised aphids were used, and that these aphids were of a size that could easily be attacked by M. paludum.*—It has already been mentioned that attacks upon very small or very large aphids were difficult to perform, and the aphids chosen for the observations were therefore of a moderate size, i.e., between 1.0 and 2.0 mm. in length.

(c) *Petri dishes were used for the observations.*—It was not found necessary to ventilate the dishes in any way, since preliminary tests, using petri dishes with muslin covers over which a current of air was directed, showed results which were similar to those in which unventilated dishes were used.

(d) *The aphids were immobilised by attaching them to sticky labels.*—The labels were numbered consecutively and arranged in the manner shown below, so that the parasite always had a choice of two different species from which it could select:

N	A	N	A	N
A	N	A	N	A
N	A	N	A	N
A	N	A	N	A

N—an individual of *Nasonovia ribis-nigri*.

A—an individual of another species of aphid.

Such arrangement was necessary to permit observation of the parasite's reaction to an aphid on its first, second or third visit, etc., and also to prevent confusion between those aphids which had already been visited and those with which the parasite was in contact for the first time. Care was taken to ensure that the aphids were attached to the labels by the terminal joints of their legs only, for if the bodies of the aphids are too close to the surface of the labels, then the parasite is unable to insert its ovipositor into the ventral suture.

(e) *Recording of results.*—The method of recording results was to write down the sequence of events as they occurred in each minute, up to a maximum of 30 minutes. Running notes on the behaviour of the parasite were recorded by means of the following abbreviations, similar to those used by Salt (1934).

Contact with an aphid for less than 2 seconds	'Touch'	T
" " " " " " period of 2-5 seconds ...	'Examination'	E
Brief insertion of ovipositor	'Jab'	J
Prolonged insertion of ovipositor (over 10 seconds) ..	'Attack'	A
Unsuccessful attack		U

Touches and examinations refer to contacts which were made by the parasite's antennae and not by the ovipositor. Under the conditions of the experiments, where the aphids are of moderate size and are immobilised, unsuccessful attacks are naturally expected to be few in number.

It is obvious that, before a parasite can examine an aphid, it first has to touch it; before making a jab, it first touches and examines it, and so on. The various reactions can therefore be considered as levels of response by the parasite,

of which an attack (or unsuccessful attack) represents the highest level. In those cases where the parasite revisited the same aphid several times during the course of an experiment, its reaction was in each case recorded in the running notes, but, for the purposes of compiling tables of results, the only reaction taken into account was that which represented the highest level of response by the parasite to that particular aphid. (For example, assuming that, in the first minute, a parasite attacked aphid No. 2, jabbed aphid No. 7, and examined aphid No. 2, and, in the second minute, it touched aphid No. 3, attacked aphid No. 4, and touched aphid No. 7, these reactions would be recorded thus:—

1st minute: A2/J7/E2. 2nd minute: T3/A4/T7.

The only reactions which would be taken into account for the aphids which had been revisited would be the Attack for No. 2 and the Jab for No. 7.)

Detailed observations.

These fall into two main groups:

- (i) Parasite given a choice between *N. ribis-nigri* and one of several other species of lettuce aphids.
- (ii) Parasite given a choice between *N. ribis-nigri* and one of several species of non-lettuce aphids (i.e., aphids of species which normally occur on plants unrelated to lettuce).

The results of these observations are given in Tables II and III. When *M. paludum* is given a choice between *N. ribis-nigri* and other species of lettuce

TABLE II.

Behaviour of *Monoctonus paludum* towards mixtures of *Nasonovia ribis-nigri* and other lettuce aphids.

No. of observations conducted	Mixture of aphids	T	E	J	A	U
6	<i>Nasonovia ribis-nigri</i> ex lettuce	0	12	10	24	0
	<i>Myzus persicae</i> ex lettuce	0	10	5	26	0
7	<i>Nasonovia ribis-nigri</i> ex lettuce	3	13	8	27	2
	<i>Aulacorthum circumflexum</i> ex lettuce	7	17	9	25	1
4	<i>Nasonovia ribis-nigri</i> ex lettuce	0	2	0	25	3
	<i>Aulacorthum solani</i> ex lettuce	0	1	2	23	1
5	<i>Nasonovia ribis-nigri</i> ex lettuce	1	4	2	32	3
	<i>Macrosiphum euphorbiae</i> ex lettuce	0	5	3	36	0
Total of 22 observations	<i>Nasonovia ribis-nigri</i> ex lettuce	4	31	20	108	8
	Other aphids from lettuce	7	33	19	110	2

T—the number of touches recorded.

E—the number of examinations recorded, etc.

aphids (*Myzus persicae*, *Macrosiphum euphorbiae*, *Aulacorthum solani* or *A. circumflexum* (Buckt.)), no preference for *N. ribis-nigri* is shown, i.e., the parasite behaved similarly towards all the lettuce aphids which were tried (Table II). If we consider all touches, examinations and jabs to be exploratory in type, thus grouping them together as 'exploratory reactions' and if we similarly group together attacks and unsuccessful attacks as 'attacking reactions,' the results may be represented graphically, and are shown in fig. 3, a.

TABLE III.

Behaviour of *Monoctonus paludum* towards mixtures of *Nasonovia ribis-nigri* from lettuce and various non-lettuce aphids.

No. of observations conducted	Mixtures of aphids	T	E	J	A	U
5	<i>Nasonovia ribis-nigri</i> ex lettuce	2	10	4	25	1
	<i>Sitobion fragariae</i> ex grass	10	20	4	3	0
3	<i>Nasonovia ribis-nigri</i> ex lettuce	1	1	1	21	1
	<i>Sitobion avenae</i> ex <i>Poa</i> grass	12	16	1	0	0
5	<i>Nasonovia ribis-nigri</i> ex lettuce	4	4	6	28	3
	<i>Brachycaudus helichrysi</i> ex pyrethrum	8	15	15	5	0
2	<i>Nasonovia ribis-nigri</i> ex lettuce	0	3	2	6	0
	<i>Aphis</i> spp. ex <i>Epilobium</i>	5	4	2	1	0
1	<i>Nasonovia ribis-nigri</i> ex lettuce	1	1	1	3	1
	<i>Amphorophora rubi</i> ex blackberry	3	4	2	0	0
Total of 16 observations	<i>Nasonovia ribis-nigri</i> ex lettuce	8	19	14	83	6
	Non-lettuce aphids	38	59	24	9	0

It can be seen, however, from Table III that the behaviour of the parasite is very different when the choice with which it is presented is between *Nasonovia ribis-nigri* (from lettuce), and other species of aphids (*Sitobion fragariae* (Wlk.), *S. avenae* (F.), *Brachycaudus helichrysi* (Kalt.), *Amphorophora rubi* (Kalt.) or *Aphis* spp.) which were taken from plants unrelated to lettuce. In this case, very few attacks were made on the non-lettuce aphids, although many of them were explored, whilst attacks upon *N. ribis-nigri* proceeded normally (see fig. 3, b).

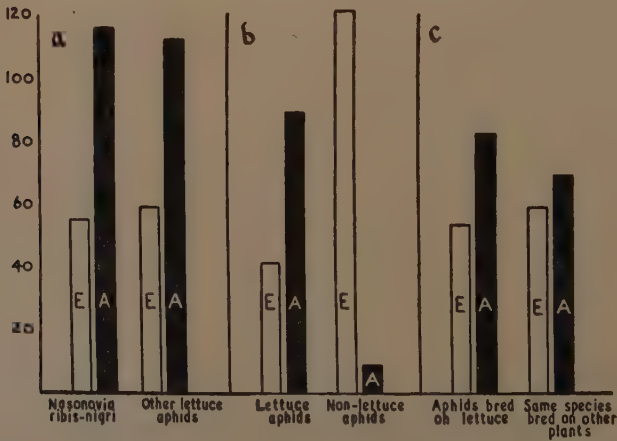


Fig. 3.—Histogram of results from Tables II, III and IV. E, exploratory reactions, i.e., touches + examinations + jabs; A, attacking reactions, i.e., attacks + unsuccessful attacks; a, illustrates results of Table II (22 observations); b, illustrates results of Table III (16 observations); c, illustrates results of Table IV (17 observations).

The main conclusion to be drawn from Tables II and III is that the usual reaction of *M. paludum* towards non-lettuce aphids, under the conditions described, is merely to examine them with the antennae and sometimes with the ovipositor, but to refrain from making an attack, whereas in the case of lettuce aphids, these exploratory actions are almost always followed by an attack no matter what species of lettuce aphid is concerned.

Supplementary observations.

These were undertaken to determine which properties of the hosts influenced their selection by the parasites.

Selection of lettuce aphids in preference to non-lettuce aphids.

In order to determine whether the selection of lettuce aphids was due to the properties of the aphids themselves or to the properties of the plants on which they had been bred, a further set of observations was carried out where the choice given to the parasite was between lettuce aphids and the same species of aphids bred on different plants. The results of these observations are given in Table IV and fig. 3, c.

TABLE IV.

Behaviour of *Monoctonus paludum* towards mixtures of aphids. Each choice is between lettuce aphids and the same species of aphid bred on another plant.

No. of observations conducted	Mixture of aphids	T	E	J	A	U
5	<i>Aulacorthum circumflexum</i> ex lettuce	3	5	11	21	2
	<i>Aulacorthum circumflexum</i> ex potato	7	14	6	8	3
5	<i>Macrosiphum euphorbiae</i> ex lettuce	1	3	3	30	1
	<i>Macrosiphum euphorbiae</i> ex blackberry	2	7	3	28	0
5	<i>Myzus persicae</i> ex lettuce	3	9	6	21	1
	<i>Myzus persicae</i> ex chrysanthemum	3	8	3	22	0
2	<i>Aulacorthum solani</i> ex lettuce	2	6	1	6	0
	<i>Aulacorthum solani</i> ex potato	1	3	2	7	1
Total of 17 observations	Aphids bred on lettuce	9	23	21	78	4
	Aphids bred on other plants	13	32	14	65	4

It can be seen that the number of attacks made upon aphids bred on lettuce plants is somewhat greater than the number of attacks made upon the corresponding aphids bred on other plants, and, in order to see whether this difference was significant or not, the data were submitted to a statistical analysis.

The analysis was made on the basis of a χ^2 test; a 1:1 ratio was assumed for attacks on aphids bred on lettuce: attacks on aphids bred on other plants for each of the aphid species concerned. For one degree of freedom the probabilities of agreement with this assumed ratio are 0.05–0.03, 0.7, 1.0 and 0.7 for the species *Aulacorthum circumflexum*, *Macrosiphum euphorbiae*, *Myzus persicae* and *A. solani*, respectively (see Table V). Furthermore, the results can be shown to be homogeneous in agreeing with the hypothesis of a 1:1 ratio; there is agreement within aphid species and between aphid species used. Therefore, so far as these limited data go, there is no evidence (except possibly in the case of *A. circumflexum* which is significant at the 5% level) that the plant on which

the aphid is bred influences host selection by the parasite. In order to obtain a complete analysis, however, it would be necessary to conduct a large number of observations in the case of each plant and, further, to improve the technique used in the observations by arranging the aphids in a random manner instead of the symmetrical fashion which has been done previously. If this were to be done, it is possible that the above statement concerning the rôle of the plant in host selection might require some modification, but there can be no doubt that host selection is due at least in part to the properties of the aphid species themselves, regardless of the plants on which they have been bred.

TABLE V.

Analysis of results from Table IV.

Host	a ₁	a ₂	n	χ^2	d. of f.	P
<i>Aulacorthum circumflexum</i>	23	11	34	4.235	1	0.05-0.03
<i>Macrosiphum euphorbiae</i> ..	31	28	59	0.153	1	0.7
<i>Myzus persicae</i>	22	22	44	0	1	1.0
<i>A. solani</i>	6	8	14	0.286	1	0.7
Deviation				1.119	1	0.3-0.2
Heterogeneity				3.554	3	0.5-0.3
Total	82	69	151	4.673	4	0.5-0.3

a₁—no. of attacking reactions performed on aphids bred on lettuce.

a₂—no. of attacking reactions performed on same species of aphids bred on other plants.

The chemical properties of the host.

That a response to chemical properties is important in host selection is evidenced by the parasite's intent examination of the cast skins of aphids, witnessed on several occasions, the empty, flattened skins having little resemblance in shape to living aphids.

However, attempts to alter the parasite's host preference by smearing aphids with the body-juices of other aphids proved unsuccessful, possibly because the extraction of the body-fluids led to their being denatured in some way. When the body-fluids of several individuals of *N. ribis-nigri* were squashed, by means of a glass rod, on to a piece of paper the parasites were not attracted to these areas but ran straight over them without even making an examination.

The influence of sight on host selection.

During preliminary observations it was noticed that the parasite was attracted to, and would stop to examine, any dark spot or protuberance on the leaf's surface. Also, when unilateral lighting was used, the parasite could be made to stop and examine the shadow cast by an aphid, one centimetre away from the aphid itself and, in other cases, where the aphids were separated from the parasites by a sheet of glass, chemical stimuli thus being eliminated, the parasites would stop and examine the glass at those places where the aphids lay directly underneath.

By observing the distance away from objects of various sizes at which the parasites gave a reaction (*i.e.*, turned away from or turned towards) it was possible to show that relatively large objects, about 4 mm. in diameter, could be perceived from approximately 6 mm. distance; smaller objects, of diameter 2.5 to 3.5 mm., could be perceived from about 3.5 to 4 mm. distance, and objects of approximately

the same size as the aphids used in the experiments (between 1.0 and 2.0 mm. in length) could be perceived at a distance of between 3 and 3.5 mm.

The influence of size and shape on host selection.

M. paludum would always stop and examine empty sessile individuals of *N. ribis-nigri* even when these had been empty for over four years. Presumably these empty sessile aphids could no longer have possessed any chemical attraction and it was assumed that, in this case, the suitable size and shape alone were sufficient to elicit an examination. Also, when the size and shape of living individuals of *N. ribis-nigri* were camouflaged, by stretching a piece of butter muslin over them, then the parasites ran straight over the top of them, apparently unaware of their presence despite their close proximity.

The influence of the plant on host selection.

Comparisons were made between the response of the parasites towards various objects attached (a) to a piece of paper and (b) to a piece of lettuce leaf. In the case of inanimate objects, such as pieces of plasticine, attached to paper, the parasite's reaction was generally to touch or examine the first few with which it came into contact and then to turn away from any others which it met. (This reaction was called an avoidance.) When confronted with the same type of objects attached to a piece of lettuce leaf the number of avoidances was less, and the number of touches and examinations was greater. It appears, therefore, as if the presence of the leaf has the effect of lowering the threshold of stimulation in these cases.

When similar observations were carried out using aphids instead of inanimate objects, the results were less convincing in that touches and examinations were of frequent occurrence with aphids attached to paper even when they were not from lettuce plants and it is difficult to elicit from the parasite, by the mere insertion of a piece of leaf, a higher level of response.

Another very noticeable characteristic of the parasite was its tendency to keep flying off the paper, whereas it remained on the piece of leaf for much longer periods of time, searching it, particularly in the hollows of the under surface.

Effect of movement on host selection.

Aphids were immobilised by anaesthetising them with carbon dioxide gas for a period of 10 to 15 minutes. The parasites failed to discriminate between anaesthetised and normal lettuce aphids, readily attacking both and thus indicating that movement on the part of the host is not an essential prerequisite to parasite attack.

Live and dead hosts.

Aphids were killed by freezing them at a temperature of -9°C . for two hours. They were allowed to warm up to room temperatures and were then used in 'choice' observations, whereupon they were readily attacked by the parasites. However, aphids that had been killed 24 hours previously received less attacks, and those that had been dead for 48 hours were not attacked at all.

Parasitised hosts.

The number of aphids that were attacked more than once was obtained from the data of the 'choice' observations. Of the 212 cases where an already attacked aphid was revisited, in only 31 was a second attack delivered; in the other 181 cases, exploratory actions were recorded. These data are taken from observations limited to a duration of 30 minutes each, and it is possible that more

attacks on hosts already parasitised would have been recorded if the observations had been extended over a longer period of time. (See Salt, 1937.)

In no instance was the emergence of more than one parasite recorded from a single host, and in those cases where two eggs are laid in the same host, only one of them develops to maturity.

Effect of waxy covering on the aphid body.

Macrosiphum euphorbiae from lettuce has a slight 'mealy' covering of wax on its cuticle and it was noticed, during preliminary observations, that the parasites appeared to spend extra time preening themselves after having come into contact with aphids of this species. In order to determine the effect of a thick mealy covering, *Brevicoryne brassicae* (L.) from cabbage was used in the following experiment.

Three fertilised females of *M. paludum* were first introduced into dishes containing medium-sized individuals of *N. ribis-nigri*, where they immediately commenced attack, evidence of their healthy condition. The parasites were then transferred to separate dishes, each of which contained 20 unparasitised individuals of *B. brassicae* of medium size. In all three dishes the reaction of the parasites was to avoid the aphids, although in the first dish one attack and one unsuccessful attack were observed and in the second dish one jab took place. At the end of 7, 10 and 15 minutes, respectively, the parasites in all three dishes showed signs of damage, falling on to their sides and backs and making vigorous attempts to rid themselves, by preening, of the waxy film with which they had become contaminated; when replaced amongst individuals of *N. ribis-nigri*, they blundered clumsily about and did not once make an attack.

However, *B. brassicae* is parasitised by certain species such as *Diaeretus rapae* (Curt.), which are apparently unharmed by the waxy secretions of the aphids. The reason for this is not clear although it may possibly be due to the fact that these parasites do not hold on to the aphids by their front legs during oviposition and lay their eggs simply by a quick stab of the ovipositor.*

Age of parasite.

It was found that the older the female, the more active she became (this interfered with the mating reaction) and that females that had been kept for 2 or 3 days away from their normal host would be seen to stab with their ovipositors at almost any object, even the glass walls of the container, as if in an attempt to oviposit.

'No choice' observations.

It was stated above that the confinement of a female parasite away from its natural host results in an increase in activity on the part of the parasite. Even if the parasite is only approximately one day old, this activity may cause it to attack a species of aphid which it would not normally attack if it is confined with this species alone, i.e., under conditions of 'no choice' of host. These attacks are neither invariable nor readily commenced but in some instances a fair proportion of attacks is observed under these unnatural conditions. It is obvious from this that 'no choice' observations are likely to produce misleading results, and it was noted that the results of replicate observations by this method often differed widely from each other.

* That the waxy covering of *B. brassicae* has a protective effect against parasites is also mentioned by George (1957) who states that *D. rapae* tends to restrict its attack to those individuals of *B. brassicae* which are at the edges of a colony. George's paper also contains interesting information regarding the oviposition behaviour and specificity of *Aphidius fabarum* Marshall, *A. matricariae* and, particularly, *D. rapae*.

Conclusions from supplementary observations.

The selection of aphids for attack by the parasite depends not only on the physical and chemical properties of the aphids but also upon the physiological state of the parasite itself. It appears that an object of suitable size and shape alone or an object possessing sufficient chemical odour alone is sufficient to elicit an examination from the parasite, but the parasite normally only inserts its ovipositor into objects that possess both these properties.

Tests of aphid species other than *Nasonovia* as hosts.

It has been seen that, in the laboratory, *M. paludum* will readily attack all species of lettuce aphids that are offered to it even when *N. ribis-nigri* is present. But, in the field, *M. paludum* was recorded only as a parasite of *N. ribis-nigri*, even in the presence, on the same plant, of other lettuce aphids. It is true that the numbers of aphids of each particular species fluctuate throughout the year (Broadbent & others, 1951), and there is a tendency for *N. ribis-nigri* to occupy the innermost leaves of the plant so that it was thought that ecological separation might be the answer to this apparent paradox. It seems inconceivable, however, that ecological separation, in this case, could ever be complete, for the distribution of aphids overlaps to some extent and it is not uncommon to find sessile individuals of *N. ribis-nigri* on leaves that carry a mixture of aphid species; in addition, in the field, adults of *M. paludum* can sometimes be collected from the outer leaves of the plant.

It therefore appears likely that the restriction of *M. paludum*, amongst the possible lettuce-aphid hosts, to *N. ribis-nigri* is unconnected with host finding or, as indicated by the results of the laboratory observations, host selection, and it was assumed, as a working hypothesis, to be due to the unsuitability of lettuce aphids other than *N. ribis-nigri* as media for the development of the parasite's eggs.

A series of experiments was set up in order to test this hypothesis. In each case 20 unparasitised, medium-sized aphids were placed on a piece of lettuce leaf in a petri dish. Into this the parasite was introduced and kept under observation for the first half hour to ensure that parasite attack had commenced. The parasite was generally removed at the end of 24 or 48 hours and the piece of leaf was replaced every second day, when it began to show signs of deterioration. The healthy aphids were transferred, by means of a fine paint-brush, from one leaf to the other but the attacked aphids were removed as they became sessile, together with the portion of the leaf to which they were clinging and were placed in separate dishes. In this way the date of appearance of sessile aphids and the date of emergence of adult parasites could be accurately recorded.

This system proved to be satisfactory in most respects although sometimes the aphids were damaged in the process of transfer from one leaf to the other.

Four experiments were conducted with each of the species *Macrosiphum euphorbiae* and *Aulacorthum solani*, and eight control dishes, containing *Nasonovia ribis-nigri* were set up, so far as possible, on the same day. In addition, five experiments were carried out using mixtures of aphids. The results are summarised in Table VI, from which it can be seen that none of the dishes containing *M. euphorbiae* or *A. solani* yielded either sessile aphids or adult parasites whilst the controls gave 11 adults (from 26 sessiles) and 5 adults (from 24 sessiles), respectively. In the mixture experiments the 20 sessiles from which four adult parasites emerged were all individuals of *N. ribis-nigri*.

These results were confirmed by other experiments in which large breeding cages were used. In this case no sessile aphids or adult parasites developed in the cages containing *Aulacorthum solani*, *Myzus persicae* or *Macrosiphum euphorbiae*, whereas 99 and 60 adult parasites, respectively, emerged from the

two control cages containing *N. ribis-nigri* over a period of approximately five months, so that these results again confirm the evidence given by field collections.

It was noted in the course of these experiments that unfertilised females gave rise to progeny comprising males only, whilst fertilised females produced both males and females with a preponderance of the latter; the average time taken for a developing parasite to produce the sessile condition of its host was approximately nine days, and a further seven days elapsed before the parasite emerged, making a life-cycle of 16 days under the conditions described and at a temperature of 22°C.

TABLE VI.

The results of laboratory experiments on breeding success in species other than *Nasonovia*.

Experiment or control	Aphid		No. of sessiles	No. of parasites
	Species	No. of individuals		
Experiment Control	<i>M. euphorbiae</i>	80	none	none
	<i>N. ribis-nigri</i>	80	26	11
Experiment Control	<i>A. solani</i>	80	none	none
	<i>N. ribis-nigri</i>	80	24	5
Using mixtures of aphids in each dish	<i>N. ribis-nigri</i>	10	} 5 (all <i>Nasonovia</i>)	2
	<i>M. euphorbiae</i>	10		
	<i>N. ribis-nigri</i>	10	} 2 (all <i>Nasonovia</i>)	1
	<i>M. euphorbiae</i>	10		
	<i>N. ribis-nigri</i>	10	} 8 (all <i>Nasonovia</i>)	none
	<i>M. euphorbiae</i>	10		
	<i>A. solani</i>	10		
	<i>N. ribis-nigri</i>	10	} 4 (all <i>Nasonovia</i>)	none
	<i>A. solani</i>	10		
	<i>N. ribis-nigri</i>	10	} 1 (<i>Nasonovia</i>)	1
	<i>A. solani</i>	10		

Locating the parasite egg.

It has been observed that the reaction of *M. paludum* towards different species of lettuce aphids is similar but the results of the experiments on breeding success in aphids other than *Nasonovia* reveal the possibility that, although the behaviour appears to be identical in all cases, the parasite may lay its eggs only in *N. ribis-nigri* and refrain from doing so in the other species of aphids from lettuce plants.

It was therefore necessary to be certain that an egg was actually laid, in these cases, and a number of different methods were explored with the object of finding the parasite egg inside the body of the aphid.

Firstly, sections and dissections of female parasites were made to determine the structure of the parasite egg (Pl. X, figs. 1 & 2). The egg was found to be oval in shape with rather pointed ends and to comprise an inner mass of cytoplasm surrounded by a distinct membrane. (The cytoplasm tends to contract away from the membrane if the dissections are carried out in glycerine.) In all cases, however, the shape of the external membrane is quite characteristic, and the eggs measure approximately 0.1 mm. in length and 0.04 mm. across at their widest parts.

Secondly, some very general examinations of transverse and longitudinal sections of aphids that had been exposed to parasite attack were made. A section of an individual of *N. ribis-nigri* which demonstrates the presence of a parasite egg is shown in text fig. 4 and Plate X, fig. 3. This particular section was a fortunate one, however, and sectioning of aphid material was a rather cumbersome method which was not pursued to great lengths.

Dissections were then made of individuals of *N. ribis-nigri* that had been exposed to attack by *M. paludum*. It was found convenient to gum the aphids to a slide with a small drop of 'Seccotine' and to dissect them, under a binocular microscope, using fine entomological needles set in glass rods. Some dissections were carried out dry, others in glycerine, others in saline solutions and others in a variety of stains. No successful results were obtained in any of these cases

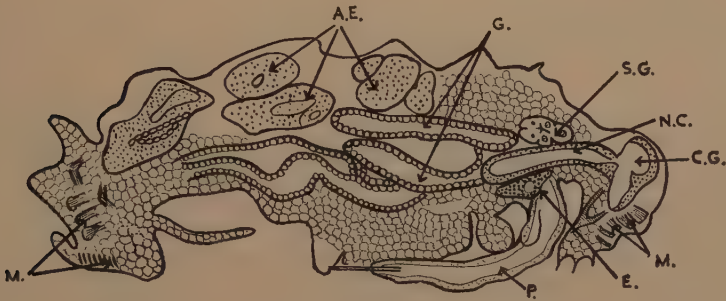


Fig. 4.—Diagram of longitudinal section of an example of *Nasonovia ribis-nigri* showing the presence of a parasite egg. A.E., aphid embryos; C.G., cerebral ganglion; E., parasite egg; G., gut; M., muscle; N.C., nerve cord; P., proboscis; S.G., salivary gland.

and the failure of these methods is probably due to the fact that, immediately an incision is made in the aphid, the body-fluids surge out, carrying with them many of the internal structures and aphid embryos of various sizes. In this way the whole of the body contents are disturbed, and a parasite egg, if present, may shift from its original site, so that however carefully the dissections are made it is always possible that the delicate egg may be ruptured. The alternative method, of cutting off the body of the aphid containing the aphid embryos behind the second pair of legs and then dissecting the thorax, yielded no better results, although this was tried on many occasions. An attempt was made to inject various stains before dissection, but here again the contents of the aphid flowed out immediately the skin was punctured.

After considerable trial and error, the technique that was finally employed was to transfer the attacked aphids to clearing fluid, a mixture of equal parts by weight of crystalline phenol and chloral hydrate melted together at low temperatures (H. L. G. Stroyan, *Aphid technique for advisory entomologists*.—*Occ. Notes Conf. Adv. Ent. Minist. Agric.* no. 8, unpublished, 1949), and to examine them daily by means of dark-ground and phase-contrast apparatus, when it was found that the contents of the aphid body would gradually clear so that it was possible to discern objects which, from their size, shape and position could be identified as parasite eggs. Similar structures were never found in aphids that had not been exposed to parasite attack.

The length of time for which the aphid has to be immersed in the clearing fluid depends on the size and coloration of the individual concerned but, in general, the egg is visible by ordinary microscopic or phase-contrast examination

after one to two days and by dark-ground illumination after two days to two weeks. Very occasionally two or more eggs were found in a single host, and it was assumed that, in these cases, they had been laid during a single attack.

The main advantage of the above technique lies in its simplicity, but eventually the parasite egg itself clears and is no longer visible. It may be possible to arrest the clearing process at the correct stage although this was not attempted and, instead, photographs were taken in order to obtain a permanent record.

The results of this clearing process in the case of *N. ribis-nigri*, *A. solani* and *M. euphorbiae* are shown in Plate X, fig. 4 and Plate XI, figs. 1-4. The parasite egg can be seen in the thoracic region of each of these aphid species although it was not possible to obtain dark-ground photographs in the case of *M. euphorbiae* as the slight waxy covering over its cuticle obscures the internal contents of the body and hinders the clearing process to some extent. The phase-contrast photographs are sufficient to show, however, that eggs of *M. paludum* are deposited in this species of aphid in the same manner as with other species of lettuce aphids that are subjected to the parasite's attack.

Discussion.

As soon as *M. paludum* finds an aphid it can exhibit either of two main types of reaction, an exploratory action followed by an attack, or, alternatively, an exploratory action only. The observed reaction towards unparasitised lettuce aphids is almost always of the former type and very rarely is a touch, examination or jab made which does not result in an attack. The experimental work shows, however, that *M. paludum* will lay its eggs in aphids in which they cannot develop and Salt (1938) mentions that there are about 50 cases recorded in the literature in which the eggs of various parasites are wasted in this manner.

There are two possible explanations for the failure of the eggs of *M. paludum* to develop in lettuce aphids other than *N. ribis-nigri*. First, the aphids may possess some active immunity such as that demonstrated by Salt in a range of different insects (Salt, 1955, 1956, 1957), and dissections, at regular intervals, of aphids that have been exposed to attack by *M. paludum* may show whether this is in fact the case. Alternatively, *N. ribis-nigri* may possess something that is vital for the normal development of *M. paludum*, which the other lettuce aphids lack. In this case, an analysis of the body-fluids of the respective aphids may provide interesting results.

When given a choice of host, the reaction of *M. paludum* towards all the non-lettuce species of aphids that were tried was merely to explore them and to refrain from making an attack, but the supplementary observations showed that, when *M. paludum* was given no choice of host, some attacks were made upon non-lettuce aphids, although these attacks were neither invariable nor readily commenced. Attacks upon non-lettuce aphids were easier to obtain from older parasites that had been kept away from their true host-species for some time, and this effect is comparable with the "lowering of threshold" mentioned by Thorpe (1948). There would appear, therefore, to be some state of balance within the parasite between the tendency to oviposit and its capacity to refrain from doing so, directed by its sense of discrimination, and in *M. paludum* this capacity to discriminate is limited to some extent, as it seems unable to distinguish, at any time, between different species of lettuce aphids.

When the parasite is given a choice of hosts, attacks upon non-lettuce aphids are extremely rare, and it is possible that this may be correlated with its egg-laying behaviour. *M. paludum* differs from other Aphidiine parasites in which egg-laying has been described in that, during oviposition, it holds on to the aphid with its forelegs and makes a *prolonged* insertion of the ovipositor, lasting some 15 seconds.

In the course of this study, some light was thrown upon the factors underlying host/parasite relations. It was the contention of Thompson & Parker (1927) that the laws underlying host/parasite relations "are not capable of expression in scientific terms nor discoverable by scientific method" and the view that they put forward was that the parasites possessed an instinct which ensured that they oviposited only in those hosts in which their eggs would successfully develop. This view cannot be accepted in the case of *M. paludum*, which deposits its eggs in aphid species, such as *M. euphorbiae* and *A. solani*, in which they cannot develop. The observations described in this paper show that the parasite exhibits a characteristic and predictable behaviour when confronted with a choice of possible hosts under carefully controlled conditions and the supplementary observations indicate that this behaviour is correlated with the physical and chemical characteristics of the host. (This is in broad agreement with the views about host selection put forward by Salt, 1935, for the Chalcidoid parasite, *Trichogramma*.)

Just what form the behaviour of a parasite will take depends on the state of the parasite itself, *i.e.*, its age, pedigree, state of nutrition, etc., and the state of the environment, *e.g.*, the presence of suitable odours, a suitable temperature, lighting and humidity and the presence of hosts of the right size, shape and activity. It seems, in the case of *M. paludum*, as if some combination of these factors is required to build up a certain 'sense-picture' (*cf.*, "mosaic sense-picture" of Ulyett, 1936), or as though a suitable chain of circumstances must occur before oviposition will commence. It seems probable that the differences in behaviour between various species of parasite are largely accounted for by the intrinsic differences in the type of 'sense-picture' that has to be built up before the parasite will react.

Summary.

A survey of the parasites of aphids that occur on lettuce was made in two localities, in the Midlands and northern England, respectively, and a list of these parasites compiled.

A study was made of the Braconid parasite, *Monoctonus paludum* Marshall, in relation to its host, *Nasonovia ribis-nigri* (Mosley), on lettuce. Techniques for observing the parasite's behaviour towards various species of aphids are described and methods of conducting experiments on breeding success in species other than *N. ribis-nigri* are given.

The oviposition behaviour of *M. paludum* differs from that of other Aphidiine parasites in which egg-laying has been described, in that it holds on to its host with its forelegs and makes a prolonged insertion of the ovipositor, lasting some 15 seconds.

It was found that the parasite did not normally attack aphids taken from plants unrelated to lettuce, and attacks upon aphids that are already parasitised and aphids that have been dead for some time, are also rare.

Aphids between 1.0 and 2.0 mm. long are of the size most suitable for attack by *M. paludum*. The parasite experiences difficulty in ovipositing in aphids that are larger or smaller than this.

The effect, on the parasite, of the waxy covering which occurs on the cuticle of certain aphid species, is described.

By immersing the aphids, which had been attacked by the parasite, in a mixture of equal parts by weight of crystalline phenol and chloral hydrate, melted together at low temperatures, it was found that the contents of the aphid bodies would clear sufficiently to reveal the presence of the parasite eggs. The preparations could then be photographed by the use of dark-ground or phase-contrast illumination, and permanent records were obtained in this manner.

M. paludum attacked and laid eggs in all the species of lettuce aphids that were offered to it, although its eggs only completed their development in *N. ribis-nigri*. The probability of *M. paludum* laying eggs in species of lettuce aphids other than *N. ribis-nigri*, under natural conditions, is considered.

The results of this study are reviewed in relation to earlier studies of a similar nature.

Acknowledgements.

I should like to express my sincere thanks to Professor H. P. Moon of Leicester University and Professor L. E. S. Eastham of Sheffield University for their guidance during the earlier part of this study and I am most grateful to Dr. C. J. Banks and Dr. C. G. Johnson at the Rothamsted Experimental Station for their initial suggestions concerning this type of problem.

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References.

- BROADBENT, L., TINSLEY, T. W., BUDDIN, W. & ROBERTS, E. T. (1951). The spread of lettuce mosaic in the field.—*Ann. appl. Biol.* **38** pp. 689–706.
- EDWARDS, R. L. (1954). The effect of diet on egg maturation and resorption in *Mormoniella vitripennis* (Hymenoptera, Pteromalidae).—*Quart. J. micr. Sci.* **95** pp. 459–468.
- GEORGE, K. S. (1957). Preliminary investigations on the biology and ecology of the parasites and predators of *Brevicoryne brassicae* (L.).—*Bull. ent. Res.* **48** pp. 619–629.
- SALT, G. (1934). Experimental studies in insect parasitism. I. Introduction and technique. II. Superparasitism.—*Proc. roy. Soc. (B)* **114** pp. 450–476.
- SALT, G. (1935). Experimental studies in insect parasitism. III. Host selection.—*Proc. roy. Soc. (B)* **117** pp. 413–435.
- SALT, G. (1937). Experimental studies in insect parasitism. V. The sense used by *Trichogramma* to distinguish between parasitized and unparasitized hosts.—*Proc. roy. Soc. (B)* **122** pp. 57–75.
- SALT, G. (1938). Experimental studies in insect parasitism. VI. Host suitability.—*Bull. ent. Res.* **29** pp. 223–246.
- SALT, G. (1955). Experimental studies in insect parasitism. VIII. Host reactions following artificial parasitization.—*Proc. roy. Soc. (B)* **144** pp. 380–398.
- SALT, G. (1956). Experimental studies in insect parasitism. IX. The reactions of a stick insect to an alien parasite.—*Proc. roy. Soc. (B)* **146** pp. 93–108.
- SALT, G. (1957). Experimental studies in insect parasitism. X. The reactions of some endopterygote insects to an alien parasite.—*Proc. roy. Soc. (B)* **147** pp. 167–184.
- STARY, P. (1959). A revision of the European species of the genus *Monoctonus* Haliday.—*Acta Soc. ent. Čsl.* **56** pp. 237–250.

- THOMPSON, W. R. (1950). A catalogue of the parasites and predators of insect pests. Section 1. Parasite host catalogue. Part 3. Parasites of the Hemiptera.—2nd edn. Ottawa, Commonw. Bur. biol. Contr.
- THOMPSON, W. R. & PARKER, H. L. (1927). The problem of host relations with special reference to entomophagous parasites.—*Parasitology* **19** pp. 1–34.
- THORPE, W. H. (1948). The modern concept of instinctive behaviour.—*Bull. Anim. Behav.* no. 7, 12 pp.
- ULLYETT, G. C. (1936). Host selection by *Microplectron fuscipennis*, Zett. (Chalcididae, Hymenoptera).—*Proc. roy. Soc. (B)* **120** pp. 253–291.
- ULLYETT, G. C. (1938). The species of *Aphidius* (Aphidiinae: Braconidae) as parasites of aphids in South Africa.—*Sci. Bull. Dep. Agric. S. Afr.* no. 178, 28 pp.

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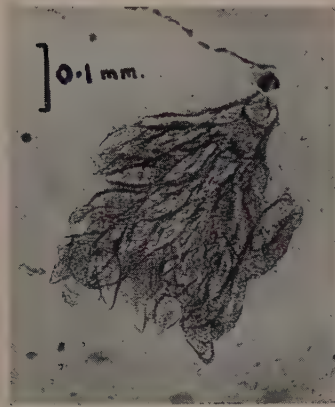


FIG. 1. An ovary of *Monoctonus paludum* dissected in glycerine, $\times 150$.

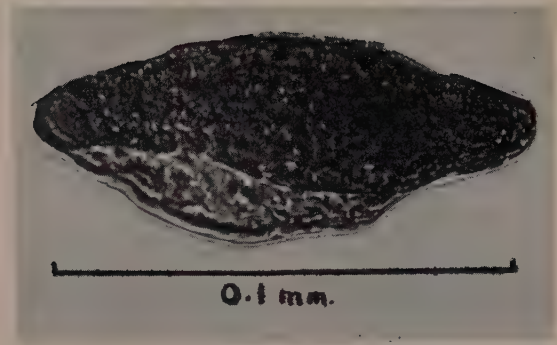


FIG. 2. Single egg of *M. paludum* in glycerine, $\times 600$.

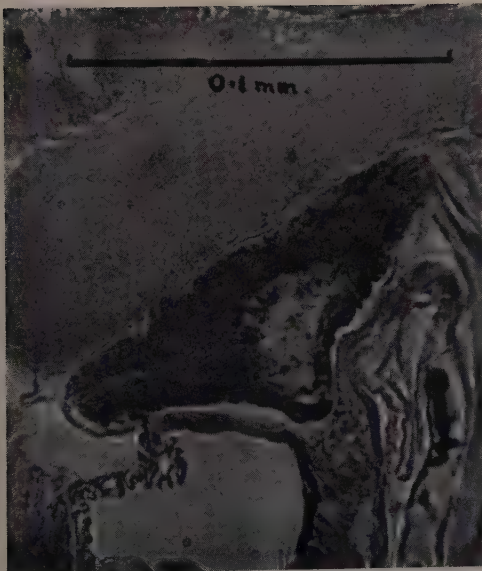


FIG. 3. Enlarged view of the egg of *M. paludum* shown in diagrammatic text-fig. 4. Stained in haematoxylin and eosin, $\times 500$.



FIG. 4. Anterior end of a specimen of *N. ribis-nigri* which has been attacked by *M. paludum*. Ventral view, $\times 150$. Clearing fluid 2 days. Phase-contrast photograph. The parasite egg (arrowed) is visible in end view.



FIG. 1. Anterior end of a specimen of *N. ribis-nigri* which has been attacked by *M. paludum*. Ventral view, $\times 100$. Clearing fluid one week. Dark-ground photograph. The parasite egg (arrowed) lies to the right of the proboscis.

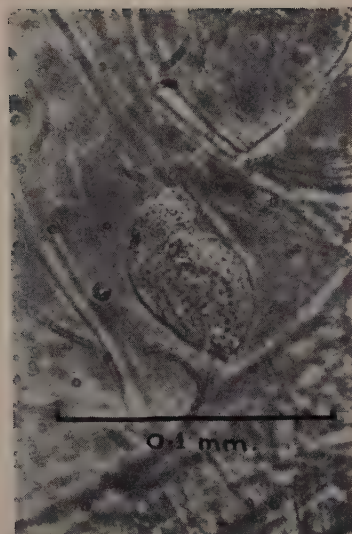


FIG. 2. Egg lying in the thoracic region, seen in ventral view, $\times 360$, of a specimen of *A. solani* which has been attacked by *M. paludum*. Clearing fluid 4 days. Phase-contrast photograph. The parasite egg lies between the first and second pairs of legs.

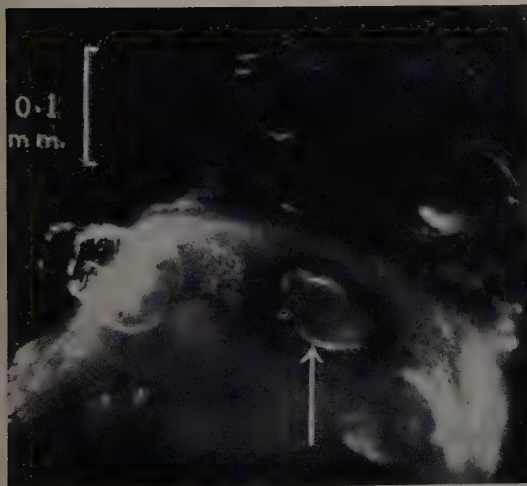


FIG. 3. Anterior end of a specimen of *A. solani* which has been attacked by *M. paludum*. Ventral view, $\times 150$. Clearing fluid 6 days. Dark-ground photograph. The parasite egg (arrowed) lies in the centre of the body just anterior to the second pair of legs.

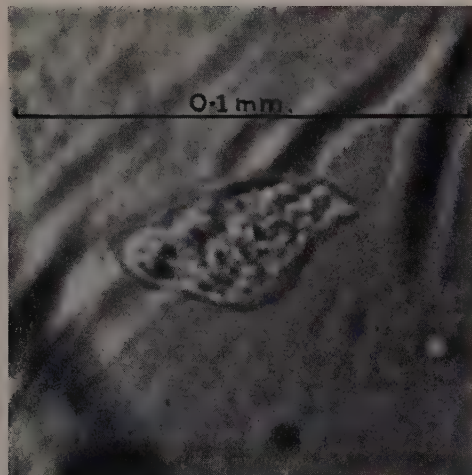


FIG. 4. Egg lying in the thoracic region, seen in ventral view, $\times 500$, of a specimen of *Macrosiphum euphorbiae* which has been attacked by *Monoctonus paludum*. Clearing fluid 2 days. Phase-contrast photograph.

INSECTICIDE STUDIES ON THE MAIZE STALK BORER, *BUSSEOLA FUSCA* (FULLER), IN EAST AFRICA.

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CONTENTS.

	PAGE
Preliminary experiments	322
Timing of first application	322
Preliminary laboratory tests with insecticides	323
Field trials, 1955	326
(a) Numbers of applications: isodrin and DDT	327
Field trials, 1956	329
(b) Dusts: endrin and DDT	331
(c) Sprays: endrin, DDT and γ BHC	333
(d) Timing of applications: DDT	335
(e) Volumes and rates: DDT	337
(f) Candidate insecticides: diazinon, malathion, DDT with resins	338
Field trials, 1957	339
(g) Comparison of DDT (dust and spray) and γ BHC (spray) with and without resins	341
(h) Comparison of DDT in emulsion at different rates of application	343
(i) Malathion in dust and spray, with and without resin	343
(j) Endrin at different concentrations, and applied to stems only	344
Aerial spraying	345
(k) DDT in an emulsion spray	346
(l) DDT in a suspension spray	346
Discussion	347
Significance of the results for control	347
The place of insecticide treatment in local agriculture	348
Summary	349
Acknowledgements	350
References	350

One of the most important insect pests of cereals in Africa is the maize stalk borer, *Busscola fusca* (Fuller). The amount of damage and average loss of yield caused by this and other species has been variously reported as from 10 per cent. (du Plessis & Lea, 1943) to 25 per cent. (Mally, 1920). Total loss of crop is not uncommon. As maize is the most important single food crop grown in Africa and is capable of giving the highest yields (Bunting, 1950), any measure which can increase the existing yields is of great potential value while the human population continues to increase.

All aspects of the problem up to 1953 have been critically reviewed by Jepson (1954), and recent work in East Africa has been covered by Walker (*in press*). A more comprehensive survey has also been made in East Africa by I. W. B. Nye

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(The insect pests of graminaceous crops in East Africa, *in press*), who has studied the species involved, their distribution and incidence in different crops, the losses caused and the occurrence of a resting stage in cereal and other hosts.

Derris was the main insecticidal material (Mally, 1920) until DDT was introduced as the major synthetic insecticide (Anderssen, 1946), and trials with the latter, chiefly applied in a dust, have now been reported from most parts of Africa. More recently, other insecticides such as endrin and the organophosphorus compounds have appeared, and other formulations such as emulsion concentrates have been used for hand, tractor and aerial spraying.

The purpose of the present trials in East Africa was to evaluate these more recent methods of control in terms of infestation rates and yields.

Preliminary experiments.

Timing of first application.

The accepted method of control by hand is the placement of a small quantity of 5 per cent. dust down the central funnel of the maize plant when it is one to two ft. high or when typical damage is seen on the leaves. Anderssen (1946) stated that the exact timing of insecticide treatment was extremely important and advised waiting up to ten days after the damaged leaves appear so that larvae could migrate from plant to plant. At this time he considered DDT to have a maximum effect. He stated that DDT lasted from two to three weeks, which, together with the delay in application, made it effective for five weeks after the first infestation.

Swaine (1957), working in Tanganyika, applied the first of three insecticide treatments three weeks after germination of the maize, or three days after the first eggs hatched on that occasion. These treatments, and others near them that are described below, were effective. Duerden (1953) applied his single treatment three weeks after sowing, thus presumably about sixteen days after germination, and obtained fair initial control. Coaker (1956) applied his first treatment four weeks after sowing or 23 days after germination (private communication), by which time there was a heavy infestation which was only controlled after three applications of DDT dust.

The relation between the degree of control and the life-cycle will be understood if the behaviour of newly emerged first-instar larvae is observed. Studies in Kenya show that they are positively phototactic. After hatching from the eggs, underneath the lower leaf sheaths, they move upwards under the influence of light. After migrating for a period of 12 to 24 hours they enter the central whorl, presumably during darkness, and begin feeding. Their position between the young leaves inside the whorl satisfies a need for darkness and pressure on opposite sides of the body. They do not penetrate the more closely packed young leaves in the axis until about ten days later. This is similar to the conditions found in South Africa by Taylor (1952) and Anderssen (1946).

It is found that first-instar larvae can be killed by placement of insecticides in the central funnel up to ten days after placing the larvae on young plants. Although control is possible, therefore, up to ten days after hatching of the eggs, maximum control is likely to take place within a few days of hatching. In the trials described below, the first treatments were applied up to six days after the eggs hatched with the result that small infestations occurred but were controlled by later applications. Spraying (with an emulsion containing 0.1% DDT) two days before infesting with first-instar larvae will also give complete control.

In the 1956 trials described below, two comparable DDT treatments in emulsion sprays, in trials (d.2) and (e.3), respectively, showed greater effect in reducing infestations when the first application was made one day before hatching of the eggs than when it was made five days after it. Endrin, however, still

gave greater control at six days afterwards. It is evident that, for maximum economic control, a highly effective persistent insecticide such as endrin, applied up to five days after the first eggs hatch, will strike a suitable balance between the two factors of maximum early kill and prolonged effect.

Events in the life-cycle have been calculated from the zero point of the date of first hatching of eggs. This is considered to be more accurate than, for instance, the dates of sowing, germination, or egg-laying. The relative times of these events will be greatly altered by the temperature and rainfall in different places. If the duration of the egg stage is known, a sufficiently practical measure of the extent of hatching of eggs will be given by the dates of first and last laying of eggs and the percentage of stems with eggs. Such possible measurements as the area under the distribution curve of egg-laying (or hatching) with time, or other parameters, would, of course, be more exact.

Preliminary laboratory tests with insecticides.

A laboratory colony of *Busseola fusca* was maintained in Nairobi and provided adequate numbers of first-instar larvae for tests and infestation experiments.

Larvae will live in cut maize stalks in cages made of wood with wire and glass walls, maintained in a constant-temperature room at about 20–23°C. Pupae were removed from the stalks and placed in muslin-covered glass fruit-bottling jars. Adults emerged and eggs were laid in the same jars, which had, however, to be covered with a glass top at the time of emergence of the first-instar larvae as the larvae will eat through cloth and nylon mesh or penetrate wire mesh. The young larvae were fed on fresh young maize leaves folded to contain them and when large enough to be confined in a cage were placed in whorled maize leaves and later inserted into holes in the ends of cut stems. No diapause occurs with this species if constantly supplied with fresh maize stalk. Breeding is difficult if the temperature rises to 25°C. and impossible at 30°C. A temperature of 21–23°C. is most suitable.

When first-instar larvae are sprayed directly or when they are confined on a deposit of insecticide for the whole of the reaction time (Potter & Way, 1958, p. 225) the response is different from that obtained when they are removed from the deposit and kept in a clean container until the response is determined. In other words, the response of the insects is complicated by the inclusion or exclusion of fumigant and stomach effects of the insecticide.

In the first tests, five first-instar larvae per replicate, five replicates per treatment, were confined on pieces of treated maize leaf, 4.5 sq. inches in area, for the whole reaction time.

TABLE I.

Percentage mortality of first-instar *Busseola* larvae after dipping in Derrisol for the dipping and reaction times stated.

Dilution	Instantaneous dipping		Dipping time in minutes		
			3	6	30
	Reaction time		Reaction time		
	24 hr.	48 hr.	20 hr.		
1 : 2000	—	—	85	95	100
1 : 1000	—	—	—	95	100
1 : 700	4	28	—	—	—
1 : 500	—	—	—	100	—
Water	0	0	0	0	0

The pieces of maize leaf were first sprayed in a Potter tower (Potter, 1952) with a mean deposit of 2.75 g./sq.m. of emulsion spray containing 2, 0.5 or 0.125 per cent. DDT or γ BHC, or 0.14 per cent. of Derrisol emulsion (equal to 1:700, the recommended field strength). They were then dried for ten minutes, insects placed on them and leaves and insects were kept in muslin-covered glass tubes, 6" \times 1", for the period stated, when response counts were taken. The results are shown in fig. 1.

Under these conditions, γ BHC appears the most toxic and Derrisol has no effect. Derrisol however, is well known to be highly toxic to *Busseola* larvae from early work in South Africa, and this was confirmed by dipping tests. Five replicates of five first-instar larvae per treatment were dipped in the dilutions in water of Derrisol stated, for the time shown. The larvae were then placed on clean maize leaves in muslin-covered tubes for recovery. The results are given in Table I and fig. 1.

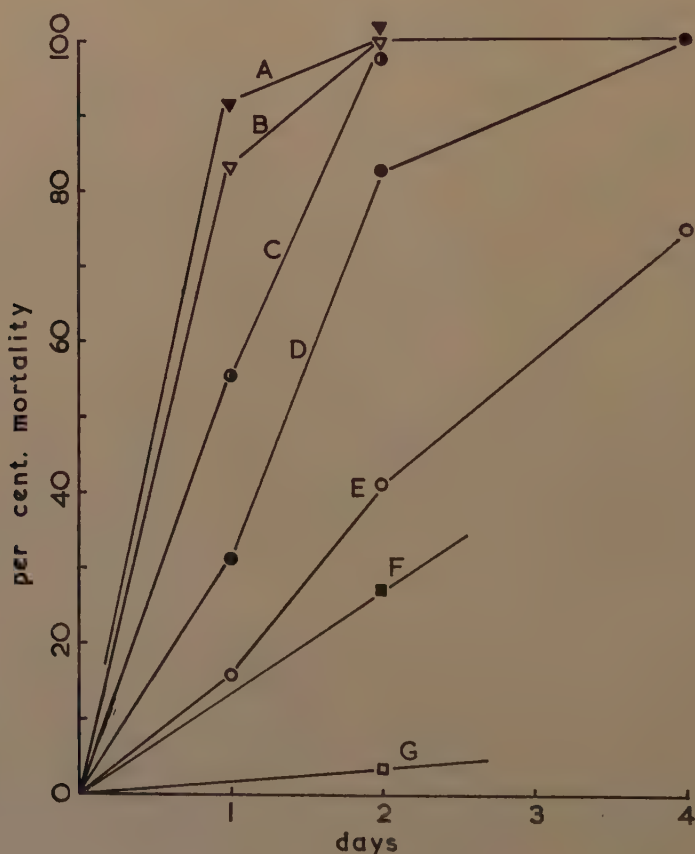


Fig. 1.—The percentage mortalities, corrected for control mortality, of first-instar larvae of *Busseola fusca* after confinement, for the period stated, on maize leaves sprayed with 2.75 g./sq.m. of emulsions containing, respectively, (A) 2 per cent. γ BHC, (B) 0.125 per cent. γ BHC, (C) 2 per cent. DDT, (D) 0.5 per cent. DDT, (E) 0.125 per cent. DDT, (G) 0.14 per cent. Derrisol. The results of dipping larvae in 0.14 per cent. Derrisol (see Table I) are also included (F).

Derrisol is thus highly effective, but only after contact with the larvae for several minutes. Such circumstances arise when larvae are bathed in Derrisol in the central funnel. The formulation has no residual effect whatever after drying.

In order to compare insecticides as residual deposits only, without complication by other effects, a method was developed in which larvae are attracted towards light across a deposit of insecticide. The deposit can be varied for a constant time in contact, or the contact time varied while the deposit rate remains constant. The responses are recorded and probit-mortality regression lines can then be drawn. Although there is some evidence for a primary and secondary response (Blackith, 1948) at very brief contact times or very low deposits, the response is linear at higher rates. The method requires further investigation and will be the subject of a later paper.

Deposits of insecticides were applied in emulsions in water to the reverse side of maize leaves. The reverse side was used to simulate the outside of the stem up which larvae first crawl and also to prevent irregularities due to the hairy upper surface. The pieces of maize leaf, about 4.5 square inches in area, were sprayed in a Potter tower, operated under the following conditions: 2 ml. of liquid

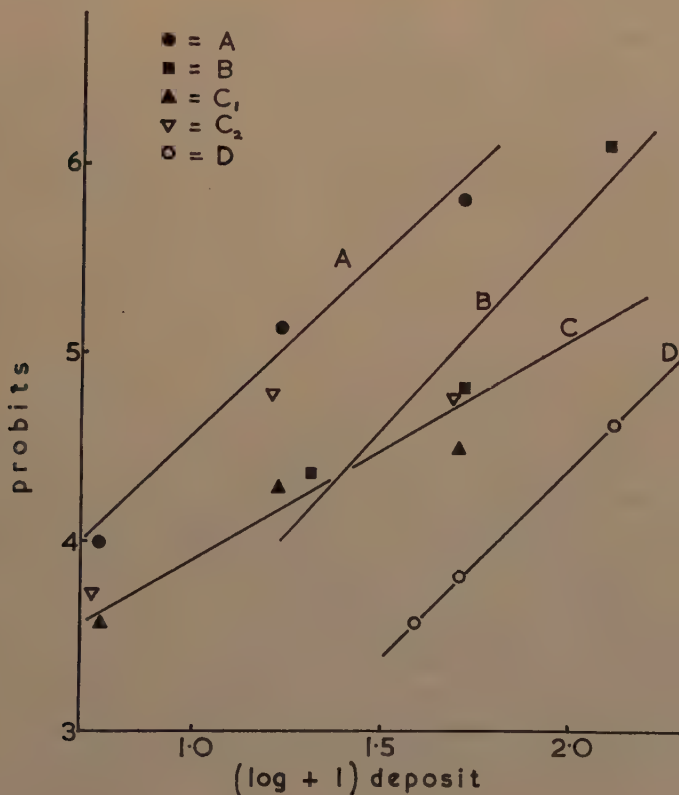


Fig. 2.—The regression of probit mortality on the log. +1 of the deposit, in mg./sq.m. (active ingredient), for first-instar larvae of *B. fusca* after one minute in contact and 20-hr. reaction time (A, B, C) and 48-hr. reaction time (D). (A) isodrin, (B) DDT, (C) endrin, (D) γ BHC.

sprayed, at an air pressure of 56 cm. mercury; plate gap 0.6 in.; mean deposit of spray over a circle of diameter 9 cm. was 2.75 g./sq.m. Leaves were then dried for ten minutes.

The results for four insecticides are shown in fig. 2 in the form of probit-mortality regression lines for constant walking for one minute in contact with the deposits. This was followed by a 20-hr. reaction time in a muslin-covered glass tube on clean maize leaf. The presence of a light below the tubes was found to be necessary to keep the larvae inside the tubes.

The following median lethal doses were read by eye from the probit regression lines.

Isodrin	:	MLD	=	1.8	mg./sq.m.
DDT	:	"	=	4.7	" "
Endrin	:	"	=	8.3	" "
γ BHC	:	"	=	about 20	mg./sq.m.

An apparent change in response led to irregularities in the regression lines for endrin and γ BHC, so the results for another test are also given for endrin (C_2). The γ BHC probit line is based on a 48-hr. reaction time as there was no response after 24 hours.

Isodrin was the most toxic material tested under these conditions. DDT and endrin were highly effective.

Field trials, 1955.

Only one replicated and controlled field trial had been reported at this time in East Africa (Duerden, 1953). Attempts had been made to obtain 'rule of thumb' methods for timing control measures, but they were not related to the main initiating factor in East Africa, the rainfall. There had, also, been no information on the relation between the level of stalk-borer infestation and the subsequent yield of the crop.

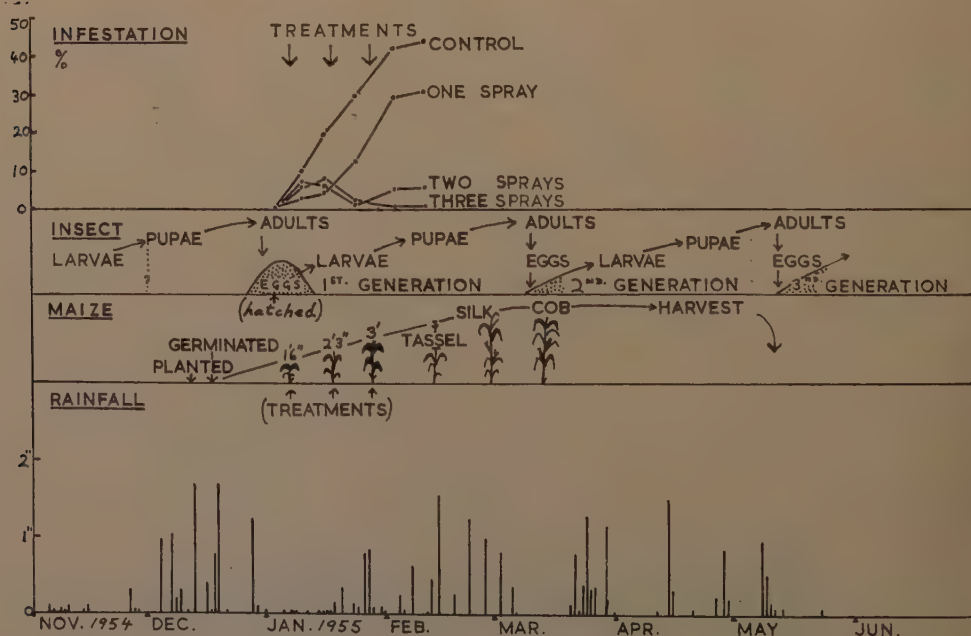


Fig. 3.—Trial (a), Mwanhala, 1954-55. The relation between insect, crop and rainfall.

Trial (a). Numbers of applications necessary: isodrin and DDT.

A trial was therefore put down at Mwanhala, Nzega, near Tabora, Central Province, Tanganyika, at an altitude of 4,100 ft., in an area where stalk borer can be expected. The laboratory and field aspects of the life-history were the concern of the Tanganyika entomologist, who carried out a nearby trial on the use of 2.5 per cent. DDT dust on African peasant holdings (Swaine, 1957).

The intention was to investigate the number of applications necessary and the effect on infestation and yield. Isodrin, a stereo-isomer of aldrin, was used, following the laboratory tests described above. The course of the trial is shown in fig. 3.

The maize, an African variety, Katumbili, was sown in 'hills' (groups of 2-3 plants) on ridged and tied rows, the hills being spaced 3 ft. \times 3 ft. apart. The seeding rate was about 7 lb./acre. There was a later intersewing of ground-nuts, as is the local custom. From a nine-acre block of maize, 25 plots, each of 400 sq. yd. (20 \times 20 yd.), were taken, separated by 1-yd. paths, and five treatments were allocated in a Latin square design, giving five replicates of each.

Sowing took place on 11th December, and the seed germinated on 16th December. This followed an initial rainfall of 2.4 in. in early December, with 1.7 in. just after sowing.

Isodrin, supplied as 19.5 per cent. emulsifiable concentrate, was used as a spray at a strength of 0.04 per cent. active ingredient (increased to 0.049% for the second and third applications). At the application rate of 9 gal. per acre this is very nearly equivalent to 0.7 oz. isodrin per acre. Except for slight scorch on a few plants where the spray had collected and evaporated in the funnels, no phytotoxic effects were seen. Spraying was by hand application from a Four Oaks 'Ross' knapsack sprayer through one low-volume swirl-plate nozzle, size 00, and applied to the plants only. The figures for gallonage per acre and amount of isodrin applied therefore need to be multiplied by about four to give these data for continuous or over-all spraying. A light wetting spray was used, not to the point of run-off.

DDT was applied at 0.05 per cent. DDT from a 25 per cent. emulsifiable concentrate.

Isodrin was applied once; twice with a ten-day interval between; and three times with a ten- and an eleven-day interval between successive sprayings. DDT was applied once only for comparison. The time taken for spraying was about two hours per acre. The maize was 1.5 ft. high at the first spraying, 2.25 ft. at the second and 3 ft. at the third.

The life-cycle in Western Province of Tanganyika has been described by Swaine (1957). Eggs were laid 11 days after germination of the maize, 31 days after 0.3 in. of rain and 53 days after the first rain of 0.1 in. Figures used here refer to the first and not the peak of egg-laying and hatching. Eggs hatched seven days after laying and the first spray was applied four days after this, or 22 days after germination of the maize, when it was 1 ft. 6 in. high. Eggs continued to be laid for a period of 17 days, after which egg-laying stopped.

The infestation rate was determined by counts of the number of hills which contained infested plants, expressed as a percentage of the total number of hills in the plot. Means were extracted for each treatment and the figures for plants with active infestation are shown in Table II. Damage which had occurred and then been controlled is not shown.

Some of these figures are seen in relation to rainfall, the state of the crop, and the treatments in fig. 3. It shows the initial rise in infestation, which continues to a peak of over 40 per cent. of hills infested in the untreated plots. One plot reached 63 per cent. of hills infested. Infestation levels were depressed

slightly by one spray of either isodrin or DDT but rose afterwards. Two applications of isodrin depressed infestations after an initial rise to 7 or 8 per cent., followed by a later rise, while three applications, again after an initial rise, maintained the infestation at below 1 per cent.

Counts of control infestation only ceased to rise appreciably at 15 days after the end of hatching of eggs. This time lag can be accounted for by the couple

TABLE II.

Mean infestation rate as a percentage of the number of hills per plot containing infested plants.

Treatment and no. of applications	Days after eggs hatched	7 days	12	21	31	38
		3	8	17	27	34
Control		10.2	18.3	27.5	42.0	43.8
Isodrin × 1 ..		3.45	4.2	12.6	29.0	31.0
Isodrin × 2 ..		7.25	6.3	1.4	5.0	5.8
Isodrin × 3 ..		6.3	8.6	2.25	0.5	0.9
DDT × 1 ..		3.5	7.8	16.9	25.0	26.7

of days migration of first-instar larvae over the plant after hatching, the time taken for signs of damage to grow out and appear, and possibly a couple of days delay in counting. There is also a small increase in control-plot infestation due to migration of larvae from hill to hill.

Second-generation eggs were laid on 9th March, by which time the maize was 6 ft. high and in cob. No detrimental effects were observed. A third generation of eggs was ready by 12th May, when the crop was harvested.

Yields are expressed as shelled grain weight, in kilos per 400-sq.-yd. plot (Table III). Unfortunately the moisture content could not be obtained.

TABLE III.

Mean shelled grain weight, in kilos per plot (400 sq. yd.).

Treatment				Yield
Control	26.1
Isodrin × 1	30.0
Isodrin × 2	40.7
Isodrin × 3	54.3
DDT × 1	30.9

Analysis of variance.

Source of variance	Sum of squares	Degrees of freedom	Mean square
Rows ..	1128.4	4	282.1
Blocks ..	2707.9	4	677.0
Treatments	2580.1	4	645.0
Residual ..	243.1	12	20.3
Total ..	6659.5	24	—

The variance ratio (F) for treatments = 31.8 for $n_1 = 4$, $n_2 = 12$, which is highly significant (5% F = 9.6). The 95 per cent. limits for the difference between means is ± 6.23 kilo/plot.

Statistically, therefore, there is no significant difference between untreated plots and those treated once with either isodrin or DDT. Two sprayings and three sprayings each gave a significant increase in grain yield.

When these figures are transformed into terms of pounds per acre and bags (East African bag = 200 lb.) per acre, the results shown in Table IV are obtained.

TABLE IV.

Yields of shelled grain per acre for the various spray treatments.

	Lb./acre	Bags/acre
Mean yield, 1 spray (isodrin) ..	798.6 \pm 166	4.0
Mean yield, 2 sprays (isodrin) ..	1251.1 \pm 166	6.25
Mean yield, 3 sprays (isodrin) ..	1445.0 \pm 166	7.2
Maximum yield obtained (3 sprays)	2380	11.9
Mean yield for controls	694.8 \pm 166	3.5

Cob weights were also recorded and closely followed the grain weights given above.

There is thus an increase of just over twice the yield of grain maize with the maximum treatment applied in this experiment, with a maximum yield in one plot of more than three times the control yield.

Remarks.

Isodrin, when applied four days after hatching of the eggs, did not completely control larval infestation immediately at the dosage applied but the infestations were reduced by the second and third sprays to below 1 per cent. of hills infested while those of the controls rose to 44 per cent. The effect of each spray lasted for from ten to fourteen days. It is interesting to note that the graphs in fig. 3 show how the second application caused the greatest reduction in infestation, the first less and the third least.

The value of a bag (200 lb.) of shelled maize was $24\frac{1}{2}$ shillings and the cost of insecticide $2\frac{1}{2}$ shillings per acre per application. Three applications would cost $7\frac{1}{2}$ shillings per acre. The mean increased yield was worth 100 shillings. As this is a peasant area, very little labour is employed, but on the other hand the economics are not strictly applicable as dusts would be used unless a sprayer could be obtained communally.

Field trials, 1956.

Trials were then laid down at Mbulu, Northern Province, Tanganyika, on maize grown under the better climatic and cultural conditions which characterise the higher yielding estate areas of East Africa.

At Mbulu (altitude 5,700 to 6,000 ft.), maize is the main food crop, although sorghum is also grown. The severity of stalk-borer attack has increased in these crops in recent years. At the same time the hilly nature of the district has necessitated the adoption of a system of soil conservation which relies on placing the dead maize stalks along the contours to form 'trash bunds.' There is consequently a large reservoir of larvae in diapause in the bunds which provides a direct source of infestation when the rains start and the young maize is growing. Unfortunately the system is simple and effective and there is no acceptable alternative. The district can therefore be expected to provide a high stalk-borer infestation every year and proves an excellent site for trials against the pest.

The predominant species is *Busseola fusca*, although a few specimens of *Sesamia calamistis* Hmps. and *S. poephaga* Tams & Bowden appeared and one of *Chilo zonellus* (Swinh.), unusual at this altitude, but which occurs plentifully in the Rift Valley, 2,000 ft. below.

The climate at Mbulu may be judged from the following figures:

Temperature: mean = 60.0°F. (08.30 hr.); 71.7°F. (14.30 hr.).

mean maximum = 74.0°, mean minimum = 55.2°.

Rainfall: average per year, 31 inches, on 90 days.

Busseola fusca passes the dry season, from June to October, in diapause as final-instar larvae in the dry maize stalks, as at Mwanhala. The rise in humidity with the start of the rains in November initiates pupation (Swaine, 1957). The pupal stage lasts an average of 28 days at Mbulu. The first pupae appeared on the 30th November, the first empty pupa cases on the 21st December, and eggs were found first on the 28th December. The first eggs hatched on the 4th January, seven days after laying. Egg-laying continued until the 28th January, after which no more were found until the next generation.

First-generation pupae appeared on the 15th February, empty cases (which implies adults) on 14th March and eggs the following day, giving a minimum larval period of about 43 days and a minimum period from egg to egg of 78 days. There will of course be considerable variation in excess of this for the duration of the various stages and the total life-cycle; the last larvae of the first generation did not pupate until the end of April. By the time that the first-generation adults were on the wing, the maize in the trials was 6 ft. high, and no eggs or larvae of the second generation could be found in the ears or tops of the stems in these plots. Observations on this generation were therefore made on other maize. The first pupae of the second generation appeared at the beginning of June when the harvest was nearly ready.

These events are more clearly shown in fig. 4, in relation to insecticide treatments and development of the crop. The numbers of larvae and pupae are

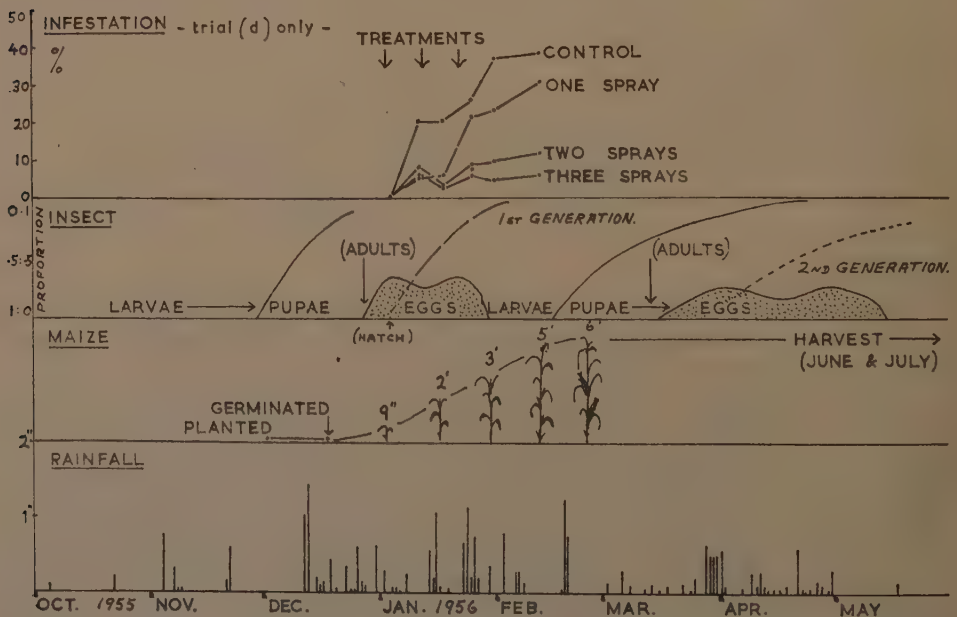


Fig. 4.—Trials (b)–(f), Mbulu 1955–56. The relation between insect, crop and rainfall.

given as proportions of each present. Egg-laying is plotted as the percentage increment per day. The presence of adults is assumed when empty pupal cases are found. A third generation would be possible in July but the rain has then stopped and the main crops have passed the stage in which they can be damaged. A few eggs can usually be found on irrigated maize in the district at this time.

Different methods have been adopted by various workers to express the degree of infestation. In the 1955 trials described above, the infestation was given as the number of hills or groups which contained one or more infested plants. In order to compare with counts of maize sown singly in rows, counts were now made of individual plants infested, not hills. Again, active infestation is recorded, and if damage is seen at the tips of the leaves but not in the centre of the whorl, the plant is not counted as showing infestation.

Maize was sown as soon as rain was imminent in order to coincide with the initial wave of *Busseola* activity and to obtain the maximum infestation possible. Sown dry on the 2nd December, rain caused germination on 17th, and the crop was about 9 in. high when the first eggs were laid. The crop was in tassel and silk before the eggs of the second generation were found. Harvest took place in early June for short-term varieties and mid-July for the later ones.

Unfortunately, four varieties of seed had to be used for different experiments, namely Kenya hybrid, Early Pearl, Yellow and White Katumbili. Sowing was in the manner advised for local peasant farmers, three seeds per hole, holes a yard apart along rows a yard apart. This amounted to about 22 lb./acre sowing rate. Cobs were either hand or machine shelled according to the moisture content. To equate yields harvested at different times and elsewhere, moisture contents were all adjusted to 14 per cent.

Plots were laid out on permanent terraces cut in the hillside and arranged in blocks, plot size differing from block to block. The largest plots, in Block A, were originally quarter-acre plots, and were divided into four experimental plots, each less than a sixteenth of an acre. Plots in other blocks, from a sixth down to a twelfth of an acre, were each divided into two experimental plots. The actual areas of maize were then measured and used to correct plot yield to pounds per acre.

A small amount of variation occurred due to losses of seeds and young plants to rats, birds, porcupines and buck and necessitated some minor corrections for plant number. Such counts were made before the plant population was affected by stalk-borer attack.

In order to separate the effects of insecticides in some of these trials, when a maximum effect was not intended, a principle of *sub-optimal* application was used. This does not appear to have been described in relation to field insecticide trials although it is well known for field weed-killing trials and laboratory estimations of insecticides and drugs. By applying treatments later and less often than is expected to give maximum effect, the responses to treatment can be separated. This is clearly seen in trial (c), when endrin is obviously superior to DDT at the strengths used. As with laboratory bioassay, it is a disadvantage if the rates or responses are not in the central region of the scale, when the results will be of little value. Once the most effective treatment is found it is also necessary to find the rates of application which give the degree of control required in practice.

Trial (b): Dusts: endrin and DDT.

Maize variety: Early Pearl.

Total area of experiment: 1.65 acres.

1st dust treatment applied: 9th January (5 days after first eggs laid).

2nd dust treatment applied: 23rd January (14 days later).

Harvested: 12th July.

Dusts used and rates were as follows:—

1. Endrin 2%	11.5 lb./acre	3.7 oz. endrin/acre
2. DDT 5%	10.5 "	8.4 " DDT "
3. DDT 2.5%	18 "	7.2 " " "
4. DDT 1%	18 "	2.9 " " "
5. Control	—	—

The difference in weight of dusts applied is due to different densities of filler. The Swaine duster (Swaine, 1954) was used to put a fine dust over the top of the plants and directed at the centre of the whorl where any excess would fall.

The statistical design was balanced incomplete blocks, with five blocks, five treatments, four per block, *i.e.*, each treatment replicated four times. Analysis is by Yates' shorter method (1936) as the efficiency is 0.94 and does not merit the use of Yates' later method (1940).

Infestation rates, as percentages, are given in Table V. They are the means of four plot counts each.

TABLE V.

Percentage infestation of maize plants treated with various dusts.

Dust		Days after hatching of eggs				
		13	21	28	34	39
Endrin	2%	6.5	1.5	1.0	0.5	0.5
DDT	5%	9.5	3.0	3.0	3.5	4.5
DDT	2.5%	6.0	6.0	5.5	5.0	5.0
DDT	1%	8.0	7.5	6.0	7.5	6.5
Control		17.0	35.5	39.0	45.0	42.0

The yields of shelled maize, corrected from 23.5 per cent. to 14 per cent. moisture content and adjusted for different plant number within blocks only are shown in Table VI. These are means of four plots each.

TABLE VI.

Yields of shelled maize per acre for the various dust treatments.

Endrin	2%	4740 lb.	23.7 bags
DDT	5%	4350 "	21.7 "
DDT	2.5%	3960 "	19.8 "
DDT	1%	3770 "	18.8 "
Control		2580 "	12.9 "

Analysis of variance of the yields.

Source	d. of f.	Variance	Significance of F
Treatments ..	4	2,493,943	greater than 0.1% (or .001)
Blocks ..	4	1,166,033	—
Error ..	11	185,521	—
Total ..	19	—	

The least significant difference, based on the 5 per cent. *t*, between any two means is ± 690 lb./acre or 3.5 bags/acre, so that there is an obvious significant increase for all treatments over the controls. There is a difference between

endrin 2 per cent. dust treatment and DDT 2.5 per cent. dust. No significant difference is demonstrable between DDT 1 and 2.5 per cent. dusts, between DDT 2.5 and 5 per cent. or between DDT 5 and endrin 2 per cent.

The increased yield factors, taking control as unity, are control, 1; DDT 1, 2.5 and 5 per cent., 1.46, 1.53 and 1.68, respectively; endrin 2 per cent., 1.83.

The maximum individual plot yield was 5,345 lb./acre (= 26.7 bags/acre) with a grain/cob ratio of 0.81, compared with a mean ratio of 0.78.

Remarks.

The economic value of trials at Mbulu is based on an approximate selling price of 30 shillings per bag of 200 lb.

Endrin, applied as a 2 per cent. dust, five days after eggs hatched, gave the highest mean increase in yield, an increase of 2,160 lb. per acre, worth 324 shillings.* In comparison, 5 per cent. DDT dust, for an outlay of 16 shillings per acre for two applications, only increased yield by 1,770 lb., worth 264 shillings; 2.5 per cent. DDT dust, applied at almost the same rate of DDT per acre as from the 5 per cent. dust, cost 18 shillings per acre (higher application rate) and gave an increase of 1,380 lb., worth 207 shillings. DDT 1 per cent. dust, costing 14 shillings, gave an increase of 1,190 lb., worth 177 shillings. These figures do not include labour.

When infestations are high but a good yield is otherwise probable, the superiority of a 5 per cent. DDT dust over one of a lower strength makes the former worth its additional cost.

Trial (c). Sprays: endrin, DDT and γ BHC.

Maize variety: Early Pearl.

Total area of experiment: 0.9 acre.

1st spray applied: 10th January (6 days after 1st eggs hatched).

2nd spray applied: 24th January (14 days later).

Harvested: 13th July.

Isodrin was withdrawn by the manufacturer after the 1955 trials, and replaced by endrin. The treatments and rates were as follows:—

1. Endrin 0.031% at 15½ gal./acre = 0.76 oz. endrin/acre.
2. DDT 0.05% " " " = 1.24 oz. DDT/acre.
3. γ BHC 0.02% " " " = 0.5 oz. γ BHC/acre.
4. Control.

All the above are emulsion sprays, prepared by diluting Endrex containing 19.5 per cent. endrin, Didimac containing 25 per cent. DDT and Gammalin containing 10 per cent. γ BHC, in emulsifiable oils.

TABLE VII.

Percentage infestation rates of maize plants.

Treatment		Days after hatching of eggs					
		7	14	19	28	34	40
Endrin	0.03%	11.0	10.0	9.0	5.0	5.5	7.5
DDT	0.05%	15.0	20.0	30.0	21.5	22.0	32.5
BHC	0.02%	—	11.0	25.5	23.5	23.5	31.0
Control	—	14.0	25.0	37.0	38.5	40.0	49.0

* No costs were available for endrin as an experimental material.

Sprays were applied by means of Four Oaks 'Ross' knapsack sprayers with one Allman no. 00 flat spray nozzle, giving a wetting spray, not to the point of run-off. The spray was directed down on the plants and was applied along rows and not overall, so that here the rates should be multiplied by two for an over-all figure.

The statistical design was randomised blocks, four blocks with four treatments, each treatment replicated four times. The trial was superimposed on a local 'method of cultivation' trial, variance due to these effects being separated in the analysis.

Infestation rates, as percentages, means of four plot counts each, are given in Table VII.

The yields of shelled maize, corrected to 14 per cent. moisture content, are given in Table VIII. They are the means of four plots each.

TABLE VIII.

Yields of shelled maize per acre for the various spray treatments.

Endrin	0.03%	3420 lb.	= 17.1 bags
DDT	0.05%	2280 "	= 11.4 "
γ BHC	0.02%	2160 "	= 10.8 "
Control		1300 "	= 6.5 "

Analysis of variance of the yields.

Source	d. of f.	Variance	Significance of F
Treatments ..	3	3,013,065	greater than 0.1% (or .001)
Blocks	3	795,336	—
Error	9	170,048	—
Total	15	—	

The least significant difference, based on 5 per cent. *t*, is \pm 660 lb./acre or \pm 3.3 bags, so that there are significant differences in response between all treatments and the control, and between endrin and DDT among the treatments. There is no significant difference between DDT and γ BHC.

The increased yield factors are, control, 1; γ BHC, 1.66; DDT, 1.75; endrin, 2.62.

Remarks.

The results of this trial show that two applications of endrin at 1.52 oz./acre (twice the dosage along the rows) overall gave the highest degree of control, as in trial (b). For a cost, based on spraying the rows only, of 5½ shillings per acre, an increased yield of 2,120 lb. per acre, worth 318 shillings, resulted. Two applications of DDT, in sprays, at 2.48 oz./acre overall, costing 1¾ shillings per acre, gave an increase of 980 lb., worth 147 shillings, while γ BHC sprays, costing 2 shillings, yielded 860 lb. per acre increase, worth 129 shillings.

Dusts at higher rates of active ingredient per acre in trial (b) reduced infestations to lower levels than the corresponding sprays even when compared after transformation to angles. On the other hand, the lower control yields in the present trial, partly due to higher infestation rates and partly to poorer growing conditions, were increased by a factor of 2.62 times with endrin *spray*, compared with 1.83 times with a higher deposit of endrin as *dust* in trial (b). It is debatable whether this would indicate a greater effect of spray than dust under identical conditions. As so many variable factors are involved, further comparison is impossible.

Trial (d). Timing of applications: DDT.

Maize varieties: i. White Katumbili, ii. Yellow Katumbili.

Total area of each experiment: i. 0.6 acres, ii. 0.5 acres.

1st spray applied: 3rd January (one day before first eggs hatched).

2nd spray applied: 12th January (9 days later).

3rd spray applied: 21st January (9 days later).

Harvested: 5th June.

Sprays used and rates:

DDT at 0.05 per cent. from Didimac 25 per cent. DDT in emulsifiable oil, equivalent to 0.98 oz. DDT/acre.

1. All three applications.
2. First and second applications only.
3. First application only.
4. Control—no application.

Sprays were applied at 12.25 gal./acre with one Allman 00 nozzle, along the rows only, as in the previous experiment.

The statistical design was randomised blocks, each maize variety covering three blocks, of four treatments per block, or three replications of each treatment per variety.

The infestation rates, as percentages, each the mean of three plot counts, are shown in Table IX. They are also to be seen in fig. 4 in relation to life-cycle and rainfall. DDT, at 0.98 oz./acre along the rows, applied three times, reduced infestations to 5.5–7.5 per cent. from control infestations of 34–43 per cent.

TABLE IX.

Percentage infestation rates of maize plants.

Treatment		Days after hatching of eggs					
		7	13	18	27	33	39
(Variety i)	1. DDT × 3 times ..	7.0	2.5	8.0	4.5	5.0	5.5
	2. DDT × 2 „ ..	7.0	2.5	10.0	11.0	9.5	10.5
	3. DDT once ..	6.0	—	19.0	26.0	25.5	35.5
	4. Control ..	20.0	18.5	27.0	40.0	34.5	34.0
(Variety ii)	1. DDT × 3 ..	5.5	3.5	5.5	5.0	6.0	7.5
	2. DDT × 2 ..	9.5	2.0	8.5	10.5	9.5	13.0
	3. DDT once ..	5.0	5.5	18.0	21.5	10.5	28.0
	4. Control ..	23.5	20.0	24.0	34.5	37.5	43.0

The yields of shelled maize, corrected to 14 per cent. moisture content and also for differences in plot areas, are shown in Table X (bag = 200 lb.).

Statistically, therefore, there is support for a difference in response between one and two applications of spray in both varieties, and also a difference between one application and the control with one variety.

The increased yield factors are:

Variety i. Control, 1; DDT once, 1.02; DDT × 2, 1.21; DDT × 3, 1.33.

Variety ii. Control, 1; DDT once, 1.19; DDT × 2, 1.89; DDT × 3, 1.44.

Remarks.

Two applications of dust or spray can be very effective, particularly if the strength is high (trials b & c). At lower strengths, three sprays may not increase

yields much more than two at higher strength, as seen by comparing trial (c), in which two sprays of DDT at 1.24 oz./acre, applied late, increased yields over the control by 4.9 bags/acre, with the present trial in which three sprays at 0.98 oz./acre, accurately timed, only increased yields by a mean of 5.1 bags. It should be remembered that slightly higher volumes of water were applied in trial (c) and that stalk-borer incidence was higher, giving a greater response to insecticides.

TABLE X.

Yields of shelled maize per acre for one, two or three applications of DDT spray.

Variety i							
Treatment				Yield			
1.	DDT 0.05%	× 3	..	4300 lb.	= 21.5 bags		
2.	DDT 0.05%	× 2	..	3930 "	= 19.6 "		
3.	DDT 0.05%	once	..	3310 "	= 16.5 "		
4.	Control		..	3235 "	= 16.2 "		
Variety ii							
1.	DDT 0.05%	× 3	..	3210 lb.	= 16.0 bags		
2.	DDT 0.05%	× 2	..	3110 "	= 15.6 "		
3.	DDT 0.05%	once	..	2660 "	= 13.3 "		
4.	Control		..	2230 "	= 11.1 "		
Analysis of variance of the yields.							
				Variety i		Variety ii	
				d. of f.	Variance	d. of f.	Variance
Treatments	3	786,067†	3	607,678‡
Blocks	2	625,570	2	185,773
Error	5*	86,560	6	39,571
Total	10*	—	11	—

* One yield calculated as missing value.

† = Significance greater than 5% (or .05). (L.S.D. = ± 620 lb./acre or ± 3.1 bags/acre.)

‡ = Significance greater than 1% (or .01). (L.S.D. = ± 400 lb./acre or ± 2.0 bags/acre.)

It is highly probable that, with accurate timing of the first application in relation to hatching of the eggs, endrin or DDT at higher strengths should give even greater increase in yield over untreated controls if only applied twice at a ten- to fourteen-day interval, provided that a high stalk-borer infestation is present. This point remains to be proved.

The duration of effect of different insecticide applications can be judged from the changes in infestation rates. These are given for trial (d) in fig. 4, where it can be seen that the first DDT spray has an effect for at least nine days, the second for about ten days and the third for about ten days. The three sprays, therefore, cover the period of increasing infestation. If fewer sprays are applied, for instance in trial (c), a spray application of endrin (1.52 oz./acre overall) is seen to remain effective for at least 14 days, compared with 7–10 days for DDT (2.48 oz./acre overall) and γ BHC (1.0 oz./acre).

Trial (e). Volumes and rates: DDT.

Maize variety: Kenya hybrid.

Total area of experiment: 1.5 acres.

1st application: 9th January (5 days after first eggs hatched).

2nd application: 23rd January (14 days later).

Harvest: 19th July.

The treatments were all emulsions, made up from Didimac 25 per cent. DDT in emulsifiable oil. (a.i. = active ingredient.)

1. DDT 0.094% a.i. at 11 gal./acre = 1.65 oz. DDT/acre.

2. DDT 0.03% " " 6½ gal./acre = 0.325 " " "

3. DDT 0.094% " " 6½ gal./acre = 0.975 " " "

4. Control—no treatment.

The upper and lower rates are equivalent to 3 pints and 1 pint, respectively, of 25 per cent. concentrate/100 gal. water, and the volume changes were obtained by the use of an Allman no. 1 nozzle for 11 gal./acre rate and an Allman no. 00 nozzle for 6.5 gal./acre. Sprays were applied as in previous spray experiments above.

The statistical design was randomised blocks, superimposed on a local manurial trial which constituted blocks. Some of these treatments involved breaking new land from fallow and gave poor stands. There was consequently considerable error variation between and within blocks that reduced the significance of the differences in yield due to insecticide treatments.

The infestation rates, as percentages, each of the mean of six replicates, are shown in Table XI.

TABLE XI.

Percentage infestation rates of maize plants.

Treatments (concentration and volume)	Days after hatching of eggs				
	13	21	28	34	39
1. DDT, high conc., high volume	7.5	2.5	3.5	4.0	7.0
2. DDT, low " low "	8.5	7.0	8.5	9.5	14.0
3. DDT, high " low "	6.5	11.5	14.0	15.0	23.0
4. Control	17.5	21.5	23.5	24.0	28.5

The yields of shelled maize, corrected to 14 per cent. moisture, and with plot yields within blocks corrected to mean plant number for the block, are shown in Table XII.

TABLE XII.

Yields of shelled maize per acre for different treatments with DDT.

Treatment	Yield
1. DDT, high conc., high volume	3290 lb. = 16.5 bags
2. DDT, low " low "	2865 " = 14.3 "
3. DDT, high " low "	2800 " = 14.0 "
4. Control	2285 " = 11.4 "

Analysis of variance of yields

	d. of f.	Variance	F
Treatments	3	1,026,606	2.8 (5% F = 3.3)
Blocks	5	5,910,583	15.9 (0.1% F = 7.6)
Error	15	371,292	—
Total	23	—	—

There is thus no significant difference detectable between insecticide treatment means, while block effects were considerable.

Yield increases over the controls are as follows:

Control, 1; DDT, high and low conc., low volume, 1.23 and 1.25; DDT high conc. and volume, 1.45.

It will not be irrelevant to give the yields resulting from certain manurial treatments in this trial (Table XIII) in order to show how they are fundamental to high maize yields before insecticide treatments are considered.

TABLE XIII.

Yields of shelled maize per acre resulting from certain manurial treatments.

Treatment	Yield
Farm-yard manure (F.Y.M.) for 5 years ..	4350 lb. = 21.8 bags
No manure for 5 years	2825 „ = 14.1 „
Newly broken ground	2180 „ = 10.9 „

The increased yield factors are:—

New land, 1; no manure for 5 years, 1.29; F.Y.M. for 5 years, 2.00.

The maximum yield recorded on one plot was 5,381 lb./acre, or nearly 27 bags/acre maize grain of 14 per cent. moisture content (from 700 plants on 266 sq. yd.).

Remarks.

Although this trial (e) is rather inconclusive, it does bring out the added control value of a higher rate of DDT compared with a change in the volume of spray. Altering the rate of insecticide at a fixed volume of 6.5 gal./acre had little effect, but increasing rates and volumes to 1.65 oz. DDT in 11 gal./acre increased yield by 2 to 3 bags/acre, worth about 70 shillings, over lower rates in 6.5 gal./acre. It should be pointed out that in this trial some block yields are low and the over-all infestation rate was also low.

The results of this trial can be compared with those of trial (c), where less insecticide than treatment (e 1), applied in greater volume of water, resulted in greater yield increase. Compared with trial (d), about the same insecticide rate as treatment (e 3), namely, 0.98 oz. DDT/acre, applied in double the volume, resulted in about the same yield increase. This seems to indicate an insecticide threshold rate below which greater volumes of water have no effect.

Further attempts should be made to carry out trials with insecticides at fixed deposit rates per acre in varying volumes of water.

Trial (f). Candidate insecticides: diazinon, malathion, DDT with resins.

Small unreplicated trials with some recently developed insecticides were put down in order to determine whether these should be included in future trials. Only infestation rates could be recorded.

Two sprays, with a two-week interval between, were applied, the first on 10th January, or six days after eggs hatched, the second on 24th. Insecticides were applied in emulsion sprays containing 0.05 per cent. active ingredient and at 15 gal./acre (one Allman no. 00 nozzle).

The treatments were as follows:—

1. Diazinon, *ex* 60 per cent. diazinon in emulsifiable oil.
2. Malathion, *ex* 50 per cent. malathion in emulsifiable oil.
3. DDT + resins, *ex* Arkotine containing 18 per cent. DDT.
4. DDT standard spray, *ex* Didimac 25 per cent. DDT in emulsifiable oil.
5. Control.

The infestation rates, as percentages, each the mean of five counts, are shown in Table XIV.

TABLE XIV.

Percentage infestation rates of maize plants.

Treatment	Days after hatching of eggs				
	14	19	28	34	39
1. Diazinon	—	2.0	5.0	5.0	14.0
2. Malathion	2.5	4.5	8.5	7.5	12.0
3. DDT + resins ..	3.0	3.0	4.0	3.5	3.0
4. DDT, standard ..	5.0	9.0	4.0	4.0	5.5
5. Control	10.0	17.0	17.5	17.5	19.0

All sprays at 15 gal./acre, containing 0.05 per cent. active ingredient, applied twice, six and 20 days, respectively, after hatching of eggs.

It will be seen that diazinon and malathion were effective for a week to two weeks after the last spray (20 days after hatching). The infestation then rose. DDT sprays were still effective for nearly three weeks after the last spray. DDT + resins was slightly more effective in controlling infestations than DDT alone.

Remarks.

Diazinon and malathion are promising active materials in that they give a high initial kill, but they have poor residual properties. Malathion may be more effective than diazinon.

The effect of resins on the toxicity of DDT films has been described by van Tiel (1952); also, Hornstein, Sullivan & Tsao (1955) and Duda (1957) have shown that greater residual effect can be obtained by incorporating an equal quantity of a chlorinated terphenyl resin in the emulsion. In this trial the incorporation of resins appeared to increase the effect of DDT, so that a DDT + resin formulation could be applied at a lower DDT strength than DDT alone. Again, results do not conclusively support this, neither do they positively disprove the lack of effect when a chlorinated terphenyl resin, 'Aroclor 5460,' is added to the more volatile γ BHC in trial (g), and malathion in trial (i) below.

Field trials, 1957.

In order to confirm several of the findings of 1956 and to investigate particularly such points as the incorporation of resins, and the use of malathion, a further series of trials was put down at Mbulu, Northern Province, Tanganyika. Although many of the trials were inconclusive on account of a heavy armyworm (*Spodoptera* sp.) attack, some of the results are of interest as repeat observations during an adverse season.

The predominant species was again *Busseola fusca* and the climate and background were similar to that described above for the 1956 trials.

The three inter-related factors on which the fate of the crop depends are the life-cycle, the state of the crop and the rainfall, and their relationships are shown graphically in fig. 5. It will be seen that the first rain, of one inch, fell on 2nd, 3rd and 4th November and that eggs were first found on swamp maize nearby on the 7th December. If the pupal period is taken to be 27 days, pupae were formed about 10–11 days after the first rain. There was a similar interval (8–9

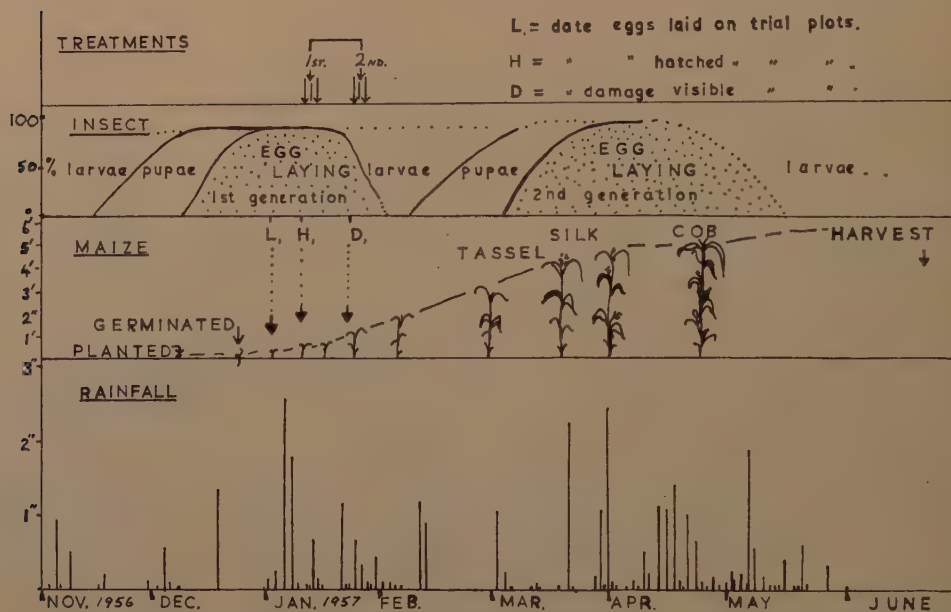


Fig. 5.—Trials (g)–(j), Mbulu 1956–57. The relation between insect, crop and rainfall.

days) after a fall of 0.75 in. in the 1956 season. The pupal period of 27 days is similar to that since obtained at 20°C. in England with laboratory cultures of *B. fusca*.

As plots were sown late on account of widely scattered rainfall, eggs were not found on the experimental maize until 3rd January when the maize was 7–8 in. high. They hatched on the 9th and 10th January. The egg-laying cycle finished about the end of January, so that the duration of the first egg-laying phase in the district is about 50 days. This is in agreement with the duration of the first egg-laying phase at Nanjara, North Kilimanjaro, where it was 44 days, but is longer than in the previous season at Mbulu, when it was 30 days. Damage was first visible in the funnels of experimental plants 10–12 days after eggs hatched, confirming the observations made in Nairobi. The maize was 1.5–2.0 ft. high at this time.

Empty pupal cases, and eggs of the second generation, were found by the beginning of March, a minimum period from egg to egg of 83 days, longer than the 72 days at a warmer place reported by Swaine (1957) but similar to the 78 days recorded the previous year at Mbulu. The period from egg to egg at North Kilimanjaro was 72 days in 1957.

Again no damage from second-generation borers was found on stems or cobs. The maize had reached four ft. in height and tassels were appearing.

Maize was sown dry on 11th–13th December 1956, but owing to an irregular rainfall, did not germinate until 25th–27th December. Fairly continual rain did not start to fall until 6th January. These long dry periods between rain may have been one of the causes of an outbreak of armyworm (*Spodoptera* sp.), following heavy 'short' rains (November) and slight 'long' rains (April) the previous year. A number of plots were completely destroyed and others badly attacked. It was impossible to continue with two of the trials, and the design of a third was upset. The absence of plants in other trials introduced errors, with consequently a high error variation which reduced the significance of many of the results. It was, of course, impossible to control the armyworm with insecticides on account of the effect on the borer population.

The first sprays and dusts were applied when the crop was 9–12 in. high, the second two weeks later at a height of 1.5–2.0 ft. Cobs were formed at the end of April and harvested at the end of June.

Variety 'Bauthman' was used and found to be a suitable short-term maize (170 days). Sowing and harvesting details were as described in the 1956 trials, namely hills of maize one yard apart, in rows one yard apart, three plants per hill.

The infestation rates are expressed as a percentage of plants attacked by stalk borer, as shown by external signs of damage. If damage was confined to the distal parts of the leaves the plant was counted as undamaged, so that the counts indicate an active infestation only.

Trial (g). Comparison of DDT (dust and spray) and γ BHC (spray), with and without resins.

The purpose of this trial was to compare the effectiveness of DDT and γ BHC and to find whether the addition of resins gave better control. The trial suffered heavily from armyworm. Owing to irregularities in the plots, the assistants also found difficulty in maintaining a constant rate of application. Rates were, however, within the range which would be expected in practice.

The treatments and rates were as follows:—

1. DDT emulsion spray (0.095% w/v DDT), prepared from 25 per cent. emulsifiable concentrate. The effective rate of DDT was 5–6 oz. DDT/acre overall.
2. DDT dust (5% DDT) at 9.5 lb. dust/acre overall, giving an effective rate of 7.5 oz. DDT per acre overall.
3. DDT emulsion spray with resin additives (0.07% w/v DDT) prepared from 18.5 per cent. DDT and resin concentrate, giving an effective rate of 4.5 oz. DDT/acre overall.
4. γ BHC emulsion spray + Aroclor resin (0.08% w/v γ BHC and 0.08% resin) prepared from 20 per cent. concentrate, giving an effective rate of 6.0–7.5 oz. γ BHC and the same of resin per acre overall.
5. γ BHC emulsion spray alone (0.08% w/v) at a mean effective rate of 7 oz. γ BHC/acre overall.
6. Control.

Sprays were applied along rows only, equivalent to an over-all rate of about 30–40 gal./acre, by hand with a knapsack Four Oaks 'Ross' sprayer, through a ceramic flat spray nozzle, size 00. Dusts were puffed by a hand piston duster over the top of the plants.

Two applications were made, the first on the 9th January, at the same time as or slightly before hatching of eggs, the second 14 days later.

Final mean infestation rates were as follows, in order of decreasing degree of control (Table XV).

TABLE XV.

Final mean infestation rates.

Treatment no.	% infestation	transformed to angles
2. DDT dust	14.5	21.8
3. DDT in emulsion + resin ..	15.3	22.6
1. " " alone ..	20.0	26.2
5. γ BHC in emulsion ..	31.0	33.7
4. " " in emulsion + resin ..	34.0	34.9
6. Control	39.2	38.7

Analysis of variance of the transformed percentages (angles).

	d. of f.	M.S.	F
Between treatments	5	227.5	3.99
Within " "	22	57.0	—
Total	27	—	—

F is significant at approximately $P = 0.01$.

The standard error of the difference between treatments 6 (control) and 1 (DDT in emulsion) is ± 5.06 ; and between 6 and 3 (DDT in emulsion with resin) is ± 4.87 . Statistically, therefore, an effect can only be detected between the control and DDT dust and DDT in emulsion with resin. The effect of DDT alone in emulsion is very nearly significantly different from the control at the 5 per cent. level of significance.

If the trend of infestation is taken as indicative of treatment effects, for which additional support is given by yields, it appears that DDT in a dust and in an emulsion with and without resin is more effective than γ BHC; that DDT in a dust and in an emulsion with resin are more effective than alone in an emulsion; and that addition of Aroclor resin to γ BHC has no effect under these conditions.

TABLE XVI.

Yields of shelled grain per acre for different treatments.

Treatment no.	Means	S.E.
3. DDT in emulsion + resin ..	3780 lb.	± 360
4. γ BHC in emulsion + resin ..	3530 "	± 440
2. DDT dust	3500 "	± 440
1. DDT in emulsion	3480 "	± 440
5. γ BHC in emulsion	3290 "	± 440
6. Control	3080 "	± 510

These figures are the means of from four to six plots. As will be seen from the standard errors, considerable within-treatment variation was present. No significant difference could be detected and no reliable conclusions can therefore be drawn from yields alone.

It will be seen, however, that DDT in emulsion with resin gave a higher yield than DDT alone in emulsion, both higher than the control yield, and that there is little difference between γ BHC in emulsion with resin, DDT dust and DDT alone in emulsion.

Remarks.

It appears that sprays of DDT alone in emulsion and with resin are at least equally effective at the rates applied, which compared a higher dosage of DDT alone with a lower of DDT with resin.

γ BHC in emulsion sprays was nearly as effective as DDT in trial (c) at less than half the application rate, but under the adverse conditions of the present trial (g), at 7 oz. per acre, it was less effective than DDT at 5-6 oz. per acre.

Trial (h). Comparison of DDT, in emulsion, at different rates of application.

There are few data available on the relative merits of one concentrated or heavy treatment and two light ones. Two treatments with DDT in emulsion were compared:—

1. One early application of 0.4 per cent. w/v DDT at 7.25 gal. per acre overall (or half this rate as continuous spray along rows), giving an effective rate of 4.8 oz. DDT per acre overall.
2. Two applications, with an interval of two weeks between, of 0.095 per cent. w/v DDT, at 10 gal./acre overall for the first, increased to 19 gal. for the second, application on account of adverse conditions. The effective deposit rate of DDT per acre was 1.5 oz. and 2.9 oz., respectively.

The actual deposit per plant in treatment 1 was found to be 0.26 mg. DDT by chemical analysis.

Although this trial was badly attacked by armyworm and was inconclusive, the results will be given. Infestation rates were found not to differ significantly, and averaged 30-35 per cent. Yield differences were also not significant, but the mean yields for the two treatments, 3680 (1) and 4140 (2), standard error ± 266 , suggest that two dilute treatments were more effective than one concentrated one. The fact that yields differed more than stalk-borer infestation rates also suggests that the treatments were having an effect on other factors, probably the degree of armyworm attack. The trial, in fact, serves to show that the application of these rates of DDT in emulsion has little effect under adverse conditions.

Trial (i). Malathion: in dust and spray, with and without resin.

Malathion has shown some promise in previous trials. In this trial, an attempt was made to compare a dust with an emulsion spray, and also to investigate the effect of the addition of a resin. Two applications were made, with an interval of two weeks, the second 16 days after hatching of eggs. The treatments were as follows:—

1. Malathion 4 per cent. dust, at a rate of 9 lb. per acre overall, giving an effective rate of 5.5 oz. malathion per acre overall.
2. Malathion 0.15 per cent. w/v in an emulsion, prepared from 50 per cent. emulsifiable concentrate at an effective rate of 5-6 oz. malathion per acre overall.
3. Malathion 0.15 per cent. w/v in an emulsion, as above, plus 6 oz. Aroclor resin per acre overall.

The mean percentage infestation rates and their values after transformation to angles are shown in Table XVII.

An analysis of variance on the transformed percentages shows a significant difference at the 5 per cent. level of probability between the control and malathion alone in an emulsion spray, with a very nearly significant difference between control and malathion spray with resin. The dust did not significantly affect the infestation, while the spray alone was more effective than spray with resin.

These differences, however, were not found at the later infestation count, when no significant differences between treatments could be detected. This would seem to indicate a persistence of malathion of not more than a week after

the last spray. Similarly, there were no significant differences between yields, which averaged between 2,700 and 3,500 lb. grain per acre. The outbreaks of *Spodoptera*, referred to on p. 339, is considered to have contributed to the inconclusive nature of these results.

TABLE XVII.

Mean percentage infestation rates.

Treatment	Days after hatching of eggs			
	19		31	
	Per cent.	Angles	Per cent.	Angles
2. Malathion spray ..	5	12.8	23	20.0
3. Malathion spray + resin	14	21.8	30	33.1
1. Malathion dust ..	20	26.4	33	25.2
4. Control	23	28.1	41	39.7
S.E.		± 2.26°		± 3.7°

In this trial, malathion appeared intermediate in effect between DDT and γ BHC, probably striking a balance between its high toxicity to stalk borer and lack of persistence on the plant. In an emulsion, at the same rate as DDT, 5-6 oz. per acre overall, malathion reduced a 41 per cent. infestation to 23 per cent. but in a 4 per cent. dust it did not significantly affect the infestation when applied at 5.5 oz. per acre. Malathion has not been shown superior to DDT dust, but in view of the inconclusive results obtained it would be well worth further trials.

Trial (j). Endrin, at different concentrations, and applied to stems only.

Further information on the action of endrin emulsion sprays was sought in this trial, and two applications of high concentration and dosage rate were compared with two of low and two of low on the stems only, the two being at an interval of a fortnight. The treatments were as follows:—

1. Endrin in a 0.15 per cent. w/v emulsion, prepared from 19.5 per cent. emulsifiable concentrate, two applications at effective rates of 4.5 oz. and 7 oz., respectively, of endrin per acre overall.
2. Endrin in a 0.037 per cent. w/v emulsion, two applications at 1.5 and 2 oz., respectively, of endrin per acre overall.
3. Endrin in a 0.037 per cent. w/v emulsion at the same rates as in treatment no. 2, on stalks only.
4. Control.

Sprays were applied at 20-35 gal. per acre for the first application and 30-37 gal. for the second, by hand as before.

The mean percentage infestation rates and their values when transformed to angles are shown in Table XVIII.

Spraying the stems only, therefore, is significantly less effective than spraying the whole plant. There is in fact no statistical difference between spraying stems only and the controls, and also none between high and low rates of application to the whole plant.

As with yields of some of the other trials, variation within treatments was too high on account of *Spodoptera* damage for conclusive differences to be obtained. Yields of grain averaged between 2,100 and 2,400 lb. per acre.

Remarks.

The reduction of infestation from 25 per cent. to 4 per cent. in the above experiment after only two applications of an emulsion spray containing 0.037 per cent. endrin applied at 1.5 and 2 oz., respectively, per acre overall compares with the effect of an emulsion spray containing 0.05 per cent. DDT at 2 oz. per acre overall (0.98 oz./acre along the rows) after three applications in trial (d) (see p. 335). At the same time, in trial (c), 1.52 oz. endrin per acre overall,

TABLE XVIII.

Mean percentage infestation rates.

Treatment	Days after hatching of eggs		
	19	31	
	Per cent.	Per cent.	Angles
1. Endrin in emulsion (high)	1	5	12.0
2. " " (low)	1	4	11.5
3. " " " (stalks only)	2.5	15	22.3
4. Control	5.4	25	29.5
S.E.	—	—	± 2.9

in 0.03 per cent. emulsion spray, reduced the infestation from 49 per cent. to 7.5 per cent. after two applications (see p. 333). Two applications of 0.095 per cent. DDT (trial (g)), however, only reduced the infestation from 40 to 20 per cent. compared with the reduction from 50 to 32 per cent. in trial (c), 34 to 10.5 per cent. and 43 to 13 per cent. in trial (d), with similar treatments. This confirms the previous conclusions that three treatments are more effective than two, and essential for a good crop under adverse conditions.

Regarding chemical recovery of spray after the first application, a mean of 0.104 mg. (1.7%) endrin was recovered from each plant in samples from treatment 1 of trial (j) after application of about 6 mg. endrin per $\frac{1}{4}$ sq. yd. After application of 2.34 mg. endrin per $\frac{1}{4}$ sq. yd., in treatment 3, 0.032 mg. per plant (1.4%) was recovered. The plants were 1 ft. high. In treatment 1 of trial (h), application of DDT in emulsion spray at about 7 mg. of DDT per $\frac{1}{4}$ sq. yd. was followed by recovery of 0.26 mg. DDT per plant (3.7%). As the mean number of plants per hill, between two and three, occupy about half the area covered by the spray, it follows that in very general terms about 95 per cent. of the spray falling on a maize hill is lost as drift, run-off, or by dripping nozzles.

Aerial spraying.

Stalk-borer control with DDT as a coarse aerosol, disseminated from an aircraft, was attempted on three maize fields at Rongai, Kenya, in May and June 1953. The experiments were carried out in co-operation with the Kenya Department of Agriculture. Although no striking results were obtained as the untreated infestations did not rise above 10 per cent., the details may be of value for later trials, one of which has since taken place.

The same technique was used in both cases. The aircraft, an Anson I, flew at regular intervals of 11 yd. over the field. A short spray boom with ten $\frac{3}{32}$ in. holes pointing forward was used for emitting the insecticide.

Filter papers (40 cm. diameter) and magnesium oxide plates were placed at 10-yd. intervals across the line of flight of the aircraft. The mass median diameters of the aerosols and chemical ground recoveries are given below for each trial.

Trial (k). DDT in an emulsion spray.

The maize was sown in groups (hills) 3.5 ft. apart, in rows, and the method of biological assessment consisted of determining the percentage of infested hills in a row. The sampled rows were selected at random.

The insecticide used was 2.5 per cent. DDT in emulsion prepared from Shell Arkotine miscible-oil concentrate.

Emission rate	12.5 gal./minute
Wind speed during application towards end of spraying	5-10 m.p.h., gusty
Average aircraft height during application	30 ft.
Average air temperature	64.8°F.
Average relative humidity	55%
Volume median diameter of spray droplets	204 microns
Number median diameter of spray droplets	81 microns
Average ground dosage of DDT	149 g. per acre
Ground recovery	69%

At the date of spraying, 27th May, the plants were 4-5 weeks old and 2.0-2.5 ft. high. Adults were laying and the time of application was about right, or perhaps a little late. The infestation developed as shown in Table XIX.

TABLE XIX.

Number and percentage of hills infested.

Weeks after spraying	Hills infested			
	Percentage		Per acre	
	Treated area	Control area	Treated area	Control area
0 (27th May)	1.1	1.1	39.2	39.2
1	1.25	2.55	44.8	91.2
2	2.9	3.1	102.8	118.6
3	3.75	7.09	133.7	252.9
4	3.6	8.03	130.6	286.1
5	3.6	9.9	129.6	353.0
6	4.34	9.15	154.7	326.1
7	4.35	9.55	156.7	340.5
8	4.04	10.38	144.2	370.0

The infestation of the control area thus increased more rapidly than that of the treated area, but final yield figures were not taken, as excessive drought affected the crop.

Secondary migrations of large larvae were found during the sixth week after spraying, and second-generation new larvae after the seventh week (16th July). After the ninth week, by which time any insecticidal effect would have disappeared, drought and thinning by the farmer ended the biological observations.

Trial (l). DDT in a suspension spray.

Here the maize was sown in continuous rows and the infestation was assessed by sampling infested plants in four random lengths of 200 yd., staggered across

the field. The insecticide used was a 2.5 per cent. DDT suspension prepared from Supona-D.

Emission rate	14.2 gal./minute
Wind speed during application	10-12 m.p.h., gusty
Average aircraft height	16 ft.
Average air temperature	59.0° F.
Average relative humidity	78%
Volume median diameter of spray droplets	183 microns
Number median diameter of spray droplets	84 microns
Average ground dosage of DDT	111 g. per acre
Ground recovery	47%

TABLE XX.

Percentage of plants infested.

Weeks after spraying	Sprayed area	Control
0	0.7	0.82
1	0.76	1.0
2	0.82	1.2
3	0.76	1.4
5	0.67	1.1

There is a slight difference between control and sprayed areas, but once again the final infestations were low, and, after three weeks, drought was reducing the counts.

Remarks.

In these experiments, maize stalk borer was, therefore, partially controlled, but due to the adverse drought conditions and the low infestation rate, it is difficult to draw any definite conclusions. Accurate timing of the insecticide application combined with respraying at two- to three-week intervals would undoubtedly improve the control and, with sufficiently heavy borer attack and favourable weather conditions, more conclusive information on crop yield would be obtained.

Discussion.

The significance of the results for control.

It has been shown that a toxic dose of endrin or DDT can be picked up by first-instar larvae walking on a fresh deposit of dried emulsion spray for as brief a contact time as one minute. Newly emerged larvae spend at least ten minutes, and often twenty-four hours, migrating up the stems and over the external surface of the plant. As their rate of progress is about one inch a minute in hot sunshine there is ample opportunity for a larva to pick up a toxic dose, provided that the insecticide deposit has not been covered by dust, has not decomposed, evaporated, or become attenuated by plant growth. Trial (j) was an attempt to find the effect of spraying the stems only. This treatment reduced the control infestation half as much as spraying the whole plant. Unfortunately the trial was statistically inconclusive, but there appears to be some effect.

An initial rise in infestation is seen in all the trials, either due to the larvae penetrating the young growing leaves inside the whorl before treatment is applied, or as in trial (d) when an application of insecticide was not sufficient to prevent them penetrating. The infestation curves fall after each subsequent treatment, indicating that larvae are being killed within the plant. When prevention of attack is occurring the curves remain steady.

In order to control larvae inside the whorl, a deposit of insecticidal dust on the surface of the plant and inside the whorl should be particularly successful as rain will tend to wash it further into the whorl and extend the period of effectiveness. Granules of endrin and DDT, which disintegrate slowly, are proving highly effective in this respect in initial trials in Kenya. Unfortunately, they arrived too late to be incorporated in the present series of trials.

Experiments with water-soluble dye, on the other hand, have shown that liquid will penetrate the tightly whorled leaves in which larvae are still present for two to three weeks after hatching of the eggs. The persistence and availability of insecticides in emulsion form can probably be increased by the incorporation of resins or other additives, and further trials may prove their value in reducing the number of applications of insecticides.

It is evident that a single spray of DDT at the usual rates is quite insufficient to control borer and adequately increase yields, and that two or three, depending on the strength, are needed if borer infestation is high. It has been suggested that a single late spray might give adequate control. In practice, the evidence indicates that late applications allow an infestation to develop which they are usually unable to control completely, resulting in a poor yield.

In general, after considering the conclusions drawn (p. 335) on duration of effect of individual applications and (pp. 334, 335, 336, 345) on rate of active ingredient per acre and the number of applications necessary, the treatments which are effective appear to be two applications of endrin spray at 2 oz. endrin per acre overall, the effect of each application of which lasts 14 days, or three applications of DDT spray at 3.5 oz. per acre, the effect of each application of which lasts 7-10 days. Late treatment requires more sprays and higher rates for effective control, as does heavy rainfall at application time.

Where a policy of trash burning and destruction is impossible, a possible method of control would be to kill or prevent the emergence of the insects in the trash bunds of dead maize stalks. Two experiments were carried out to find whether the application of a heavy spray of DDT in emulsion would prevent adult moths emerging into cages placed over sprayed dead maize stalks. Ants attacked the treated and control heaps, however, and no emergence in the control cage occurred. In view of the distances adult moths migrate and the difficulty of spraying widely scattered trash bunds, the method may, of course, prove impracticable.

The place of insecticide treatment in local agriculture.

The degree of infestation of a crop nearly always depends on the time of sowing. If crops are sown so that their susceptible stage, from nine in. to three ft. high, coincides with the beginning of the primary hatching of eggs, the maximum infestation will develop, while a crop sown later may escape completely. For example, a crop sown in the Moshi district on 8th November suffered 46 per cent. infestation, while a plot sown alongside three weeks later was only attacked to the extent of 7 per cent. The main objection to taking advantage of this fact is rainfall. If sowing is delayed until the attack is expected to be light, the early rainfall may have stopped, or the stage when the crop is still susceptible to drought may coincide with the falling-off in rainfall. It is a common maxim that the earliest sowings have the highest yields, other factors permitting, in most types of rainfall régime. If this is the case, the use of insecticides will allow sowing at the optimum time for maximum yield.

Finally, a comparison between the effect of stalk-borer control and the effect of good agriculture on yields is enlightening. In trial (a), the average yield where stalk borer was controlled was 7.2 bags of shelled maize per acre. On some plots, however, situated on old termite mounds, yields were often higher, and in one case reached 11.9 bags per acre. This is probably due to fertilisation

and introduction of minerals into the soil. Compared with these figures, the average local yield in African maize is less than 2 bags per acre. The biggest problem in Western Province agriculture is therefore to increase yields by attention to such agricultural practices as sowing and manuring, and the greatest value of insecticides might be for obtaining a yield for subsistence purposes, rather than as a cash return.

In trial (e), the increase in yield due to stalk-borer control can be compared with that resulting from applying farm-yard manure for five years. The response is about the same. The importance of obtaining the maximum yields by good agricultural practice, including improved varieties, is obvious. On higher-yielding crops, however, the added increase from stalk-borer control is of great value both as food and for the cash return on which a raised standard of living depends.

Conclusions on the importance of stem borers in a region with such varied climate and agriculture as East Africa cannot be drawn from isolated trials. The present series show that they must be repeated for at least three, and if possible five, seasons before a reliable assessment can be made.

An analysis of the relation between infestation and yield based on these trials is in the press (Walker, The relation between infestation by the maize stalk borer, *Busseola fusca* (Fuller) and yield of maize *), and a discussion of the distribution of infested plants and sampling methods at the same place as trial (a) is in preparation.

Summary.

Trials in East Africa (chiefly in Tanganyika) are described to show that the time taken for first-instar larvae of *Busseola fusca* (Fuller) to reach the more closely packed young leaves in the central axis of the maize plant is about ten days, and that insecticides are effective up to the end of this period. Results show that the best time for control is as near hatching of the eggs as possible, but with more persistent insecticides such as endrin, economic control is possible up to five days later.

A method of testing insecticides as residual deposits, by allowing first-instar larvae to walk on them, is given, and it was found that isodrin, DDT, endrin and γ BHC are highly effective as residual films. The MLD's for one minute in contact are 1.8 mg./sq.m. for isodrin, 4.7 mg. for DDT, 8.3 mg. for endrin and about 20 mg. for γ BHC. Derris emulsion has no residual effect after drying and is only effective in the liquid state after contact with larvae for several minutes.

In a series of field trials over three years, increases in yield of up to 2.6 times the control yields were shown to be possible, and averaged twice the control yield. Endrin was the most consistently effective insecticide, applied as a 2 per cent. dust and as a 0.03–0.04 per cent. emulsion spray. Two applications of endrin at an interval of two weeks were effective, but, for DDT, three applications of an emulsion containing 0.05 per cent. DDT at nine-day intervals were more effective than two while one may be of little value. An application of 2.5 oz./acre of DDT can be effective for 7–10 days, while 1.5 oz./acre of endrin can be effective for 14 days. In general, however, rates per application should not fall below 3.5 oz. DDT or 2 oz. endrin per acre, overall.

The superiority of a 5 per cent. DDT dust over one of 2.5 or 1 per cent. makes it more economical in a high-yielding, heavily attacked area. Diazinon and malathion in emulsion sprays are less persistent than DDT.

Trials with 4 per cent. malathion dust and 0.15 per cent. malathion emulsion spray were inconclusive on account of heavy damage by *Spodoptera* sp.

* To appear in *Ann. appl. Biol.* 48 no. 4, 1960.

Attempts to increase the persistence of malathion and γ BHC by the addition of chlorinated terphenyl resins were also inconclusive, but DDT in emulsion, with resin, appeared more effective than DDT alone.

The economics of successful control measures at the prices obtaining at the time are discussed under the various trials.

Chemical estimations of the deposits of insecticides retained on the plants showed that between 1.4 and 3.7 per cent. of the quantity applied per unit area can be recovered in this way.

In a discussion of the significance of the results in control, it is suggested that spraying the stems only is half as effective as spraying the whole plant.

The conditions and results relating to two aerial spray trials are given.

The place of control of *Busseola* in agricultural practice is described, and some of the present results are quoted to show that yields can be increased by good farming practice as much as by control of *Busseola*.

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References.

- ANDERSSON, E. E. (1946). Controlling the maize stalk-borer with DDT.—*Fmg in S. Afr.* 1946 repr. no. 63, 2 pp.
- BLACKITH, R. E. (1948). Primary and secondary responses in biological assay.—*Nature, Lond.* **161** pp. 20–21.
- BUNTING, E. S. (1950). Maize, the highest yielding cereal.—*World Crops* **2** pp. 5–9.
- COAKER, T. H. (1956). An experiment on stem borer control on maize.—*E. Afr. agric. J.* **21** pp. 220–221.
- DUDA, E. J. (1957). The use of chlorinated polyphenyls to increase the effective insecticidal life of lindane.—*J. econ. Ent.* **50** pp. 218–219.
- DUERDEN, J. C. (1953). Stem borers of cereal crops at Kongwa, Tanganyika, 1950–52.—*E. Afr. agric. J.* **19** pp. 105–119.
- HORNSTEIN, I., SULLIVAN, W. N. & TSAO, Ching-hsi. (1955). Residual effectiveness of mixtures of organic phosphorus insecticides with chlorinated terphenyls.—*J. econ. Ent.* **48** pp. 482–483.
- JEPSON, W. F. (1954). A critical review of the world literature on the lepidopterous stalk borers of tropical graminaceous crops.—127 pp. London, Commonw. Inst. Ent.
- MALLY, C. W. (1920). The maize stalk borer, *Busseola fusca*, Fuller.—*Bull. Dep. Agric. S. Afr.* no. 3, 111 pp.

- DU PLESSIS, C. & LEA, H. A. F. (1943). The maize stalk-borer, *Calamistis fusca* (Hmps.).—*Bull. Dep. Agric. S. Afr.* no. 238, 51 pp.
- POTTER, C. (1952). An improved laboratory apparatus for applying direct sprays and surface films. . . .—*Ann. appl. Biol.* **39** pp. 1-28.
- POTTER, C. & WAY, M. J. (1958). Precision spraying. In Shepard, H. H. Ed. *Methods of testing chemicals on insects* **1** pp. 154-258. Minneapolis, Minn., Burgess.
- SWAINE, G. (1954). A simple and inexpensive insecticide duster.—*E. Afr. agric. J.* **20** pp. 38-39.
- SWAINE, G. (1957). The maize and sorghum stalkborer, *Busseola fusca* (Fuller), in peasant agriculture in Tanganyika Territory.—*Bull. ent. Res.* **48** pp. 711-722.
- TAYLOR, F. (1952). The maize-stalk borer in the eastern Orange Free State.—*Fmg in S. Afr.* **27** pp. 450, 452.
- VAN TIEL, N. (1952). Improvement of the residual toxicity of DDT solutions by the addition of coumarone resin.—*Bull. ent. Res.* **43** pp. 413-419.
- WALKER, P. T. (*in press*). The progress of stalk borer control in East Africa.—*Proc. 4th int. Plant Prot. Congr., Hamburg 1957*.
- YATES, F. (1936). Incomplete random blocks.—*Ann. Eugen.* **7** pp. 121-140.
- YATES, F. (1940). The recovery of inter-block information in balanced incomplete block designs.—*Ann. Eugen.* **10** pp. 317-325.

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BIOLOGY AND ECOLOGY OF THE GARDEN CHAFER,
PHYLLOPERTHA HORTICOLA (L.).

VII.—THE FLIGHT SEASON: MALE AND FEMALE
 BEHAVIOUR, AND CONCLUDING DISCUSSION.

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A general description of mass behaviour of the garden chafer, *Phyllopertha horticola* (L.), in the flight season was given earlier in this series (Milne, 1958). The outstanding features are two roughly equal and half-overlapping phases of activity: Phase 1, the swarming of the beetles over the grass sward, followed by Phase 2, the swarming on the surrounding bracken, hedges and trees. Investigation of sex proportions and mass reproductive state in the two phases permitted some deductions as to individual male and female behaviour (Milne, 1959*a, b*). In the present paper, further details of behaviour are given, and study of the flight season is concluded with a brief general discussion.

Behaviour in phase 1.

Swarming.

Previous writers have remarked on the swarming of garden chafers over the grass sward (Phase 1) without attempting to analyse it (see Milne, 1958). For the first day or two of the season the beetles above ground are all males (Milne, 1959*a*). The characteristics of swarming are the same then as later when females appear, namely, a feverishly busy concentration of individuals alternately weaving in flight close over the ground and alighting to run around. Only males behave in this way. Females are far less feverish; they do not take part in the weaving flight; instead they perambulate slowly on the ground and, being generally very heavily outnumbered by males, tend to be quickly immobilised through pairing (Milne, 1959*a*). Females, in fact, do not swarm, they are swarmed upon! Swarming over the grass is essentially a male activity. It is a concentration of sexually excited males searching for emerging females.

Individual female activity in the swarm is described more fully later on. The male runs energetically upon the grass, pausing briefly now and then (usually to swing his head from side to side but occasionally to clean it with his forelegs) and running on again. When he decides to fly he often takes off from the tip of some taller stalk or blade in his path. The flying is always close over the ground, the average height being about 9 inches. In cooler flying weather, a flight usually consists of a single flat arc varying from 1 to 20 feet in length; in hotter weather, it is a weaving back and forth in short arcs before landing to run on again.

Siting and coherence of the swarm.

Spatial distribution of garden-chafer grubs is very patchy and irregular (Gray, Peet & Rogerson, 1947; Raw, 1951). If the distribution in a field has been mapped by systematic sampling just before the flight season (to be dealt with

* Agricultural Research Council Unit of Insect Physiology.

in Part VIII of this series), it will be found that swarming is always confined very accurately to the infested areas of sward even when these show no obvious differences from the uninfested parts. Now, the male starts searching for females immediately on his emergence above ground; and his activity is characteristically random, so that progress in any direction is more or less cancelled out by that in the opposite direction (Milne, 1958). This, together with gregariousness, would be sufficient to explain the confinement of swarming to infested areas, but only if the male always rested at night where he swarmed during the day. However, about a week after his primary emergence he takes to spending the night on the surrounding bracken, hedges or trees (Milne, 1958, 1959a). Thus, as Phase 1 progresses, some males have to find their way back to the infested areas each morning. It seems likely they are guided by the swarming of other males which, having made their primary emergence later, do not yet leave the infested sites at night. This seems likely because the male exodus from bracken, etc., never begins until after swarming has actually started on the infested sites each morning. Guidance may be a matter of auditory, visual and olfactory stimuli. Certainly the sound and sight, the buzzing and the swirling, of a swarm are very striking to the human senses; and, at close range, the beetles have a somewhat rank odour. Such stimuli may also play a part in keeping the swarm coherent. None of these suggestions was tested, apart from a somewhat trivial experiment involving beetle odour (below).

Beetle odour is easily demonstrated by stoppering ten individuals of either sex in a 4-oz. bottle for a few minutes. Male odour seems to be different from and is certainly stronger than female odour. The following experiment, on the question of attraction of male odour for males, was made on a sunny day.

Two contiguous square yards, (A) and (B), were inconspicuously marked off with thin wire at a random site on the infested sward. A $4 \times 4 \times 0.5$ in. envelope (a), of ballet net dyed a dull green, containing 15 males, was then placed at the centre of (A). Beetles (naturally all males) were continually alighting, running and taking off in (A) and (B). After three minutes the numbers of males walking on (a), (A-a) and (B) were snapshotted simultaneously. The envelope was then transferred to the centre of the square yard (B), which for easiness in recording was now regarded as (A), and the snapshot count again taken after three minutes. This procedure was repeated at three other random sites, giving eight trials in all. The results are shown in Table I.

TABLE I.

Field experiment on the possible attraction of male odour to other males.

Trial	Male beetles on			
	B	A	A-a	a
1	3	3	1	2
2	1	4	3	1
3	2	4	4	0
4	3	1	1	0
5	1	4	4	0
6	4	1	1	0
7	0	1	1	0
8	2	2	1	1
Totals	16	20	16	4

(See text for explanation of a, A & B.)

Although more males visited (A) than (B), the difference is not statistically significant. But the total of 4 beetles on the envelope (a) is significantly high in comparison with the total of 16 on the remainder of the square yard (A-a). When a male alights in (A) the chance that it will be found upon any particular 4×4 in. section is $1/81$ if all sections are equally attractive or unattractive. With 20 males alighting, the mean expectation per section is $20/81$ or 0.247 male with standard error $20/81 \times 80/81$ or 0.494 . The difference between observed and expected for the section covered by the envelope therefore gives a normal deviate of $(4-0.247)/0.494$ or 7.6 . A deviate of this magnitude could only occur if the envelope section had some extra-attractive power. Two conclusions are possible: either the concentrated male odour or the appearance of the envelope itself provided the extra-attractive power. The first of these alternatives is more likely, but a more ingenious experiment would be required to prove this conclusively.

Sexual recognition.

In their random running and flying, males are obviously searching for females. When the male pauses in his running around on the grass he not only swings his head from side to side but also spreads open the palmate clubs of his antennae. The female does similarly as she walks around sedately. Yet it is very doubtful if either sex can recognise the other except at very close quarters.

Observations of natural, undisturbed behaviour were made in the field. Among hundreds of observations of male passing female at distances of $0.5-6.0$ in., both to windward and leeward of her, only twice could the behaviour be interpreted as possible evidence of recognition at a distance. In both cases, the distance was less than one inch and the male was downwind from the female, the wind being light.

In the first instance, the male and female were approaching, and would have passed each other, on approximately parallel routes about 0.9 in. apart across the wind. At the moment when the male came opposite the female downwind, he slewed round and, accelerating, made straight to clasp her.

In the second instance, the female was sitting still upon a broad blade of plantain, three or four inches above the ground. The male flew past within $0.5-0.8$ in. on the same level and downwind from her. He checked his flight about 6 in. farther on, turned smartly, landed close beside her on the blade and clasped her immediately.

In these two instances, there would seem to be some grounds for belief that the male sensed the presence of the female at a distance of rather less than one inch when downwind of her. At the same time, the apparent reaction could easily have been nothing more than a fortuitous change of direction and speed that was lucky. In some other cases, under similar circumstances of distance and wind direction, the male has proceeded on his way apparently oblivious of the female presence.

There is no doubt, however, that one beetle recognises the sex of another from the briefest tactual exploration. Because all individuals are making incessant random changes of direction, beetles are frequently colliding on the sward. At each such collision, the participants immediately begin to scramble agitatedly all over each other. If both are males, they part almost at once to resume searching; but a male and a female pair immediately.

In observing phase-1 activity one soon reaches the conclusion that pairing in a garden-chaffer population really depends practically entirely upon chance physical encounters (collisions) between individuals. It is a surprisingly efficient method. One sees relatively very few unpaired females on the sward, and most of these become paired off in a remarkably short time. The success of the method is due to the preponderance of males and their tireless energy. Males preponderate in

Phase 1 partly because they are actually more numerous (53-65% of the entire adult population), partly because their population emergence curve begins earlier and partly because unlike females they are, weather permitting, active daily over the sward after their primary emergence (Milne, 1956, 1959a). As will shortly be seen, females spend much of their time below ground in Phase 1 after their primary emergence. Their behaviour was studied minutely on the close-grazed *Agrostis-Festuca* sward (1-3 in. deep including thin basal mat, average 2 in.) which garden chafers typically infest.

Time required for female to be discovered.

When a female comes up to the sward surface, she may sit still for a moment or two but usually starts right away to walk around with intermittent rests. Her course, like that of the male, seems to be entirely random. The direction frequently changes so that now she may be proceeding zig-zag this way and next she is circling to go that way. But her slow, sedate, unexcited progress over the grass is in striking contrast to the feverish haste of the male. As already noted, she is 'discovered' when a male collides with her. The question is how long is a female at large before she is discovered? The time elapsing before her discovery, *i.e.*, the 'discovery time,' will obviously depend on (a) chance, (b) weather and (c) density of males around.

(a) With both sexes apparently moving at random within the swarm area, discovery time for a female must be to some extent a matter of chance. At one extreme she may chance to emerge under the very feet of a running male (I have seen this happen on two or three occasions), in which case discovery time is *nil*. At the other extreme she may, *in cool weather*, still not be discovered after half an hour or more of walking and pausing on the sward, in which case she re-enters the turf undiscovered that day.

(b) Discovery arises mainly from male searching activity, the intensity of which depends directly on male body temperature. The higher their body temperature the faster male beetles move, therefore the more collisions per unit time and hence the shorter the average discovery time. Body temperature, being governed by weather, is highest in sunny, calm conditions.

(c) It scarcely needs saying that the more males per emerging female on unit area the shorter the average discovery time.

TABLE II.

The time elapsing between the emergence of a female upon the sward surface and her discovery by a male.

Number of individual females observed	Average male density (and range) per sq. yd.*	Discovery time
13	8.1 (2.3-16.0)	0-60 sec.
6	5.0 (1.2-8.7)	2-14 min.
6	0.9 (0.3-2.3)	> 14 min.**

Data for 25 females observed in nature.

* The square yard centred upon the female; 4-10 readings per female; readings spread over period between her emergence and discovery except when discovery took only seconds; in latter case readings extended to 2 min. after discovery.

** Observations broken off at between 15 and 25 min. and females still undiscovered.

Male density is the most important factor. That is obvious in Table II which, although chance and weather effects are not eliminated, still reveals a negative correlation between male density and female discovery time.

In the Table II sample, taken in different seasons and to investigate contrasting conditions, the mean discovery time (among the 19 females seen to be discovered) was 2 minutes. Short though 2 minutes may seem, it is nonetheless an overestimate because the sample is unduly weighted with observations made at low male densities such as occur at the beginning of Phase 1 or in poor activity weather. The great majority of female discoveries are made at higher male densities, as can be verified in Milne (1958, 1959a). A mean discovery rate of 1 minute or a little less is very probably nearer the truth for Phase 1 as a whole in most seasons. Even in the present sample, 6 of the 19 females were discovered in less than 30 seconds.

Distance travelled by female before being discovered.

If a female flies, then she can, of course, be many yards away from her emergence point before a male finds her. But, in fact, it is rare for a female to fly before her discovery. The following is the only combination of conditions under which such flying was ever seen to be fairly common: a male density of less than 1 per 3 sq. yd., the sun shining brassily from a cloudless sky, and a shade temperature greater than 21°C. (70°F.), this last indicating the absence of a cooling breeze. These conditions can result in nearly half of the females being undiscovered long enough for their body temperature to be raised sufficiently by solar radiation for them to fly. Of seven females observed to fly under such conditions, and which were not discovered before leaving the sward altogether, the general picture was: they walked slowly at first, accelerating gradually until in the end they began to make flights of rapidly increasing duration. The first flight was no more than a flutter of a few inches from the tip of a stem to the ground, the next a distance of a few feet, the next anything from 5–100 yards ending on the bracken or trees. The first flutter occurred at the following intervals after emergence: 2, 3, 3, 4, 6, 8 and 12 minutes, mean 4.4 minutes. The flights were more or less straight.

Cloudless sky and shade temperature greater than 21°C. occurred on only 6 of 115 days comprising the total duration of Phase 1 over five seasons. Yet on only 2 of these 6 days was the density of active males sufficiently low for flying to be fairly common, and it must be remembered that if active males are few then emerging females are much fewer. Practically always then (113 of 115 days) male density is too high or sunshine too intermittent or shade temperature too low (11–21°C.) for flying before discovery to be anything but fairly uncommon. Flying before discovery is obviously the reason for so-called 'aberrant' females (see p. 374). The important point here, however, is that on emerging upon the sward most females are discovered (paired) before they have opportunity to fly.

In walking randomly around before her discovery a female may traverse an actual path varying from less than an inch up to several feet, depending on how long she is at large and on the weather conditions at the time. On a straight line, however, the point at which she is discovered (P = paired) is on the average only a few inches from her emergence point (E) on the sward. A sample of 22 females observed in the field gave a mean of 4.5 inches, range 0–30 inches (Table III). But this sample was also unduly weighted with observations at the (rarer) low male densities, hence the mean of 4.5 inches is very probably somewhat high.

Mating before female has laid all or most of her eggs.

When a male discovers a female on the sward he immediately mounts and clasps her. Until she has laid 70–100 per cent. of her eggs (as shown by dissection)

the female reacts in a very prompt and definite way to being clasped. The moment the male is firmly on her back, she carries him down into the sward until just out of sight from above—under some overhanging stems or a leaf. There she stops. This was observed in 43 out of 44 cases in nature. (The

TABLE III.

Horizontal distance from the emergence point (E) of a female to the point (P) where she is discovered by (and paired with) a male. Distance measured as the straight line joining (E) to (P).

Distance (in.)	<1	1-5	6-10	11-20	21-30
No. females	10	6	3	2	1

Data from 22 females observed in nature.

exceptional female completed her mating on the surface of the sward and burrowed into the soil immediately afterwards.) Very occasionally the observer may barely discern the hinder ends of the male elytra after the female has stopped. But in the vast majority of cases the mating pair is hidden entirely from above, and the female goes no deeper than is necessary just to conceal. If at all possible her descent is vertical. In 34 of the 43 cases the concealment point (C) was immediately under the point (P) where the male found and paired with her. In the remaining 9 cases, vertical descent from (P) was impossible owing to the nature of the sward; the females here had to seek around, taking the first accessible route slanting downwards; in these cases the straight-line distance between the verticals through (P) and (C) varied from 0.5-4.0 inches. Table IV shows

TABLE IV.

Horizontal distance from the discovery (pairing) point (P) of a female to the point (C) where she conceals herself and the clasping male. Distance measured as the straight line joining (P) to the vertical through (C).

Distance (in.)	0.0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0
No. females	34	2	2	1	0	1	2	0	1

Data from 43 pairings observed in nature.

the full data. For the whole sample of 43 pairs the mean distance between the verticals through (P) and (C) was 0.3 inch, the range being 0.0-4.0 inches. Clearly the first reaction of the female to the male's clasping is to carry him at once into concealment immediately below where he finds her.

The act of concealment generally takes only a few seconds. Although the male attempts it from the moment of clasping, coition rarely begins until the

TABLE V.

Duration of coition in 29 pairs in nature.

Duration (min.)	4-8	9-13	14-18	19-23
No. pairs	4	15	8	2

female settles down at the concealment point. It is a quiet affair, accompanied by little or no movement after insertion of the penis (see Rittershaus, 1927, for fuller details). Coition lasts 4-23 minutes, average 12 minutes (calculated on ungrouped data, Table V). Its end is invariably decided by the female. She vigorously shakes and shrugs the male off her back by twisting her body and thrusting with her upturned hind legs. Usually she gets rid of him at the concealment point (23 in 31 cases studied). Occasionally, however, after struggling vainly for a while, she is obliged to carry him to the sward surface and struggle around there before getting rid of him (remaining 8 cases). This appears to be necessary when there is too little 'elbow room' for the female at the concealment point.

The discarded male resumes at once his feverish search over the sward for another mate. His late partner, on the other hand, immediately descends as vertically as possible to the sward base where she straightway begins to dig herself into the soil. The verticals through (C), the concealment point, and (D), her point of entry into the soil, usually practically coincide (19 in 31 cases), unless the female in descending from (C) is deflected by some vegetational obstruction (4 cases), or unless she has had to bring her male to the surface (8 cases) and so diverge from (C) before beginning to descend. It is in the latter 8 cases that the biggest discrepancies between (C) and (D) occur. Nevertheless, over all 31 cases the average distance between the verticals through (C) and (D) was only 1.1 inches (Table VI).

TABLE VI.

Horizontal distance from the concealment point (C) of a female and her clasping male to the point of entry into the soil (D) of the female. Distance measured as the straight line joining (C) to the vertical through (D).

Distance (in.)	0.0	0.5	1.0	1.5	2.0	3.0	7.0	12.0
No. females	19	1	5	1	2	1	1	1

Data from 31 pairings observed in nature.

At (D) the female digs vertically downwards into the soil. She is a powerful digger but her effort is spasmodic, there being frequent rests. Performance varies widely from female to female. One took 31 minutes to sink just out of sight in the soil, and 42 minutes later it was 2 inches below the soil surface. Another took 1.5 hours to descend to a depth of 0.5 inch (measured from its hind end). Still another had attained a depth of only 0.25 inch after 4 hours.

Clearly, points (P), (C) and (D) lie close together and in fact usually coincide for the female with all or the greater part of her eggs yet to lay. The horizontal straight-line distance (E) to (D) was also measured in 22 cases (Table VII), *i.e.*,

TABLE VII.

Horizontal distance from the emergence point (E) of a female (with all or most of her eggs yet to lay) on the sward to her point of re-entry into the soil (D) after mating. Distance measured as the straight line joining (E) to the vertical through (D).

Distance (in.)	<1	1-5	6-15	16-25	>25
No. females	2	13	3	2	2

Data from 22 females observed in nature.

the distance from the point at which she emerges (E) on the sward surface to the point at which she returns (D) into the soil after mating. This distance ranged from 0-29 inches, with mean 7.2 inches (calculated on ungrouped data). Since this short distance is characteristic until oviposition is complete or nearly complete, it is obvious that the typical female deposits most of her eggs in practically the same place as she herself passed her larval existence.

The plan view (to scale) of the relation between points (E), (P), (C) and (D) for a representative selection of females (11 of the 22 individuals in Table VII) behaving naturally on the sward are given in fig. 1. For convenience, individuals are all shown as setting off eastwards from (E) but, of course, they actually set off in all directions. No attempt is made to indicate the erratic course pursued between points.

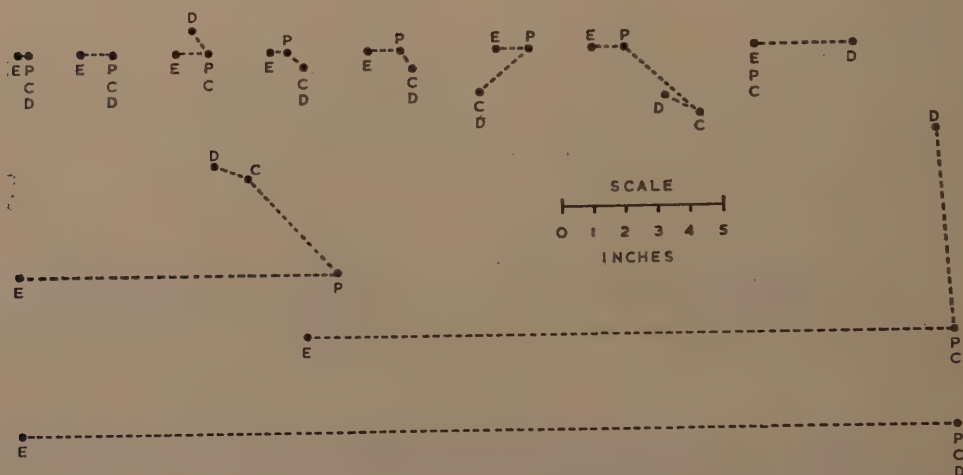


Fig. 1.—Plan view of linear relations between emergence point (E), pairing point (P), concealment point (C) and point of entry into the soil (D) in eleven females (a representative sample) with all or most of their eggs yet to lay.

Mating after female has laid all or most of her eggs.

With a female emerging upon the sward after 70-100 per cent. of her eggs has been laid, the behaviour on being discovered by a male is quite different. This has been observed in a large number of females and may be summarised as follows:

The almost-spent female comes up on the surface of the sward and walks around until discovered. Mating lasts the usual time but there is no concealment, *i.e.*, the pair rests quietly on the sward surface throughout coition. This finished (penis withdrawn), the female makes no attempt to get rid of the male. Instead she ambles around over the grass carrying him, still clasped on her back, for 5 to 30 minutes. When the male finally leaves, apparently of his own accord, she does not return into the sward. She continues to walk around with occasional short rests and short flights (2 or 3 yards). At the end of 10 to 20 minutes she flies to the nearest bracken (or trees), perhaps ten to fifty yards away. If discovered by another male before that time has elapsed, she repeats the procedure of unconcealed mating followed by carrying him around on her back and later wandering by herself over the sward, before flying off to the bracken. There she mates again, and, towards the end of the day's activity, begins to feed—for the

first time as an adult. She is now in Phase 2 and either returns to the sward next day or later as a 'bee-liner', or remains on the bracken until she dies.

There are no unconcealed matings at the beginning of Phase 1 and practically no concealed matings towards its end. This is to be expected since lack of mating-concealment is the mark of the spent or almost-spent female.

Other habits of female until most of her eggs are laid.

It would obviously be impracticable to provide, by direct observation in the field, sufficient data on all the details of individual female life after primary emergence on the sward. As a compromise, females were studied in glass jars (2-lb. size) under conditions closely simulating the natural. Even so, the data took three years to accumulate because of the difficulty of acquiring females in the act of making their primary emergence in nature. About one-third of the experimental females were collected at large in the field on the first female-day of each of three flight seasons; the remainder resulted from 'farming' a random sample of female pupae in the sward of a small caged area of Upper High House Field (see Milne, 1958). Since all available females were taken in both cases, the total sample would be expected to contain primary emergers with fat-body scores 3, 2 and 1 in natural proportions, namely, 25, 50 and 25 per cent., respectively (see Milne, 1959*b*, Table III), score 1 denoting the most advanced stage of reproductive development.

When found making her primary emergence, a female was transferred immediately to a jar with a male. A separate jar was provided for each female. The jar contained a 2-inch layer of fresh soil (max. particle size 2 mm.) for oviposition. On top of the soil was a fitted disc of fine *Agrostis-Festuca* turf about one inch deep and including only the top 0.125 inch of soil in which it grew originally. This turf came from the natural habitat of the garden chafer. In the jar, it tended to dry a little with resultant slight toughening, so the disc was cut into four quadrants to ensure, if necessary, easy access to the soil below. All this left a 2.5-3 inch air space above the turf. The jar bottom and its sides up to about 0.5 inch from the top surface of the turf were painted black to keep out light. An elastic band running vertically round the bottom, sides and mouth of the jar prevented the lid, a petri dish, from fitting so closely as to hinder free exchange of air.

The jars were kept outdoors, shaded from direct sunlight by the north wall of the field laboratory but subject to the full light of the sky. In this situation, over-heating and humidity complications from the sun were avoided. Temperature conditions at 1-1.5 inches depth in the soil in jars and in the field are compared for a period of 23 days in Table VIII. The mean of daily maximum temperatures (°C.) in the jars was 15.9 (range 9.4-21.7) and in the field 15.8 (11.7-21.1), i.e., reasonably similar. Means of daily readings at 0800-0830 hours, respectively, 10.1 (5.8-12.6) and 11.8 (10.0-13.9), suggested (as do details in Table VIII) that the daily minimum in jars was somewhat lower than in the field, although jars were covered with sacking during the night. On the whole, however, temperature conditions in the soil of the jars approximated fairly closely to those in the field.

As soon as primary mating was completed, the female invariably dug down out of sight in the jar (just as in the field—see earlier) and was no more seen that day. The male, now searching over the surface of the turf disc, was then taken out. During each day of the experiment, the jars were examined at 15 or 30 minute intervals from 0800 to 1600 hours G.M.T., half an hour being about the minimum time that an unmated female will stay on the surface when not in direct sunlight. Every time a female re-emerged on the turf, the eggs she had laid (if any) were removed and she was allowed to re-mate. This was accomplished speedily and without undue disturbance as follows. First the turf was

gently lifted out with the female resting on it (unlike many insects, the garden chafer seems quite undisturbed by, *i.e.*, shows no reaction to, the near approach of forceps and the human hand); then the 'used' soil was poured upon the egg-sieve and fresh soil substituted; the female was now returned on her piece of turf to the jar and a male added; after mating the male was always transferred immediately to one of three stock cages (a male never being used more than three times).

TABLE VIII.

Differences of temperature conditions at $1\frac{1}{2}$ in. depth in the soil in experimental jars (A) and in nature (B).

Day	Differences ($^{\circ}\text{C}.$) for A-B	
	Daily maximum temperature	Temperature at 0815 hr.
4 June	+ 4.4	—
5 "	+ 0.6	—
6 "	— 2.9	— 3.3
7 "	— 0.8	— 2.5
8 "	+ 2.6	— 4.2
9 "	— 1.6	— 2.7
10 "	+ 0.5	— 2.3
11 "	— 0.2	— 1.5
12 "	— 0.1	+ 0.7
13 "	+ 2.0	— 0.2
14 "	— 0.4	+ 0.5
15 "	— 0.9	— 0.3
16 "	— 2.3	— 1.7
17 "	— 1.9	— 0.6
18 "	— 2.7	— 1.7
19 "	— 0.7	— 4.6
20 "	+ 1.2	— 2.6
21 "	+ 3.4	— 0.6
22 "	+ 0.2	— 0.7
23 "	+ 0.2	— 1.6
24 "	— 0.3	— 2.3
25 "	+ 0.1	— 2.0
26 "	—	— 2.1
Mean difference per day	+ 0.06	— 1.73

A female did not usually surface every day and never more than once in any day. Her second mating was invariably followed by immediate disappearance back into the soil. Subsequent matings might or might not be followed by immediate disappearance; but any female remaining on the surface for more than a minute or two after mating had usually, as dissection showed, already laid more than 70 per cent. of her eggs, and had always laid at least a few eggs. Females which remained for hours on the surface had practically finished ovipositing and obviously would have entered Phase 2 (on the bracken) if that had been possible.

As a rule, the experimental female came up (on the turf surface) and went down (into the soil) some time within the period when beetles were active in the field on that day. Occasionally an individual came up in its jar earlier or later than the first or last beetle in nature but always well within the maximum limits of daily activity, *i.e.*, 0800–1600 hr. G.M.T. (Milne, 1958). On two days (only), a few females appeared on the turf surface in their jars when no beetles at all appeared on the sward in the field. This is not surprising, however, since these two days were showery, cold and blustery. Besides being rain-free and calm,

conditions in and on the turf within the sheltering jar were warmer than in or on the sward in nature.

For each female, the days on which she came up and the number of eggs laid between her 'upcomings' were recorded. Females were killed at various combinations of total upcomings and total eggs laid. They were then dissected to see how many fully-formed eggs remained. A total of 46 females was used in the experiment. Of these, 6 died naturally; they had laid no eggs and no reliable information on egg-content could be got owing to internal decomposition. The remaining 40 were deliberately killed at one of their upcomings and complete data for them are shown in fig. 2. It should be noted that five individuals

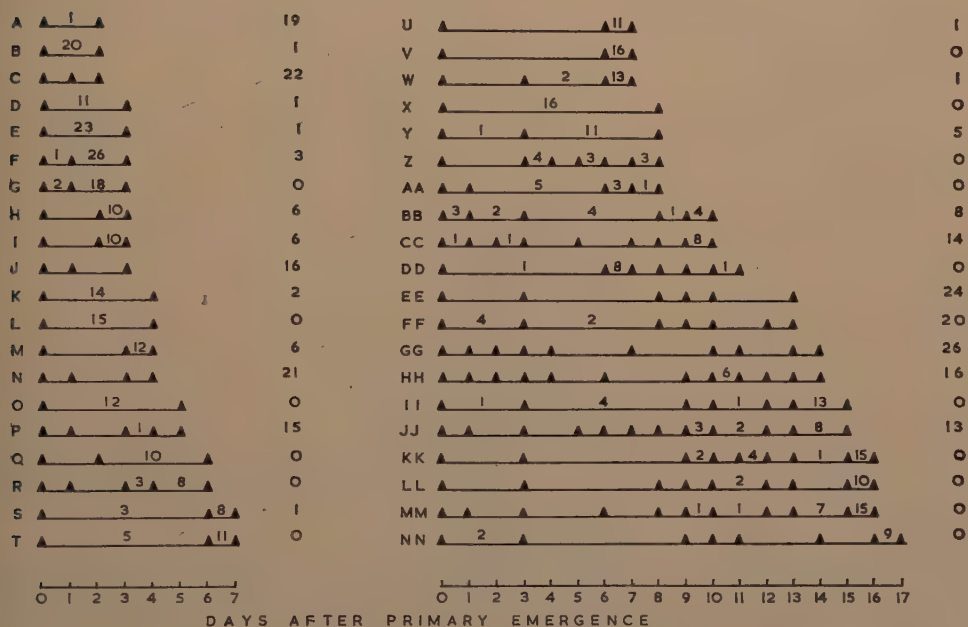


Fig. 2.—Behaviour of the female during the period between primary emergence and the laying of the last egg. Data for 40 females, labelled A–NN. Day 0 is the day of primary emergence. The horizontal line shows how long (in days) the particular female was allowed to live. The arrow-heads (black triangles) denote 'upcomings,' i.e., the days on which the female emerged upon the turf surface and was mated. The number of eggs (if any) laid between each pair of upcomings is entered between the appropriate arrow-heads. The number out to the right of each horizontal line shows how many eggs remained to lay when the female was killed.

(C, J, N, EE & GG) laid no eggs; the remainder laid from 5–100 per cent. of their eggs (Table IX). None of the 40 females had any fat-body remaining when killed. Thus, each individual had produced its full complement of eggs. This ranged from 9–30 with mean $708/40 = 17.7$ eggs. All the residual eggs (248) were fully formed, and very few (10) were not ready to be laid (3 in individual A, 2 in H, 3 in J, 1 in N and 1 in EE).

The average egg-production of 17.7 suggests that the 40 individuals comprise a representative sample of natural population (*cf.* Milne & Laughlin, 1956). Moreover, as pointed out earlier, there is every reason to believe that the distribution of fat-body scores at primary emergence would be the same as in nature.

TABLE IX.
Some details derived from fig. 2.

Female	Fraction of eggs laid before killing (%)	Number of upcomings before oviposition started ¹	Days after primary emergence before		Number of ovipositions ⁶	Number of upcomings during oviposition period ⁷	Total upcomings before end of oviposition ⁸
			Oviposition started ³	70-100% of eggs laid ⁵			
A	5.0	1	1.0	—	—	—	—
P	6.3	3	3.5	—	—	—	—
FF	23.1	1	1.5	—	—	—	—
HH	27.3	8	10.5	—	—	—	—
CC	41.7	1	0.5	—	—	—	—
JJ	50.0	8	9.5	—	—	—	—
H	62.5	2	2.5	—	—	—	—
I	62.5	2	2.5	—	—	—	—
BB	63.0	1	0.5	—	—	—	—
M	66.7	2	3.5	—	—	—	—
Y	70.6	1	1.5	8	3	2	3
K	87.5	1	2.0	4	2	1	2
F	90.0	1	0.5	3	3	2	3
D	91.7	1	1.5	3	2	1	2
S	91.7	1	3.0	7	3	1	3
U	91.7	2	6.5	7	2	2	3
W	93.6	2	4.5	7	3	2	4
V	95.9	1	1.0	2	3	1	3

G	100-0	1	0-0	3	2	1	1
L	100-0	1	2-0	4	1	0	1
O	100-0	1	2-5	5	1	0	1
Q	100-0	2	4-0	6	1	0	2
R	100-0	3	3-5	6	2	1	4
T	100-0	1	3-0	7	2	1	2
V	100-0	2	6-5	7	2	0	2
X	100-0	1	4-0	8	1	0	1
Z	100-0	2	3-5	8	3	4	6
AA	100-0	2	3-5	8	3	2	4
DD	100-0	1	3-0	11	3	5	6
II	100-0	1	1-5	15	4	5	6
KK	100-0	3	9-5	16	4	5	8
LL	100-0	5	11-0	16	2	3	8
MM	100-0	6	9-5	16	4	4	10
NN	100-0	1	1-5	17	2	6	7
Range	5-0-100-0	1 - 8 ^a	0-5-11-0 ^d	2-17	1 - 4	0 - 6	1 - 10
Mean	—	2-1	3-6	7-9	2-3	2-0	3-8

Notes: ¹ Includes primary emergence. ² Female GG came up 10 times without starting. ³ Mid-point of the two upcomings between which the first eggs were laid. ⁴ Females EE & GG had still not started after 13 & 14 days, respectively. ⁵ Assuming (on the basis of other experiments) that females came up immediately after laying the last egg. ⁶ Number of lots in which eggs are laid, lots being separated by one upcoming or more. ⁷ Excluding the upcoming immediately before the first and the upcoming immediately after the last lot of eggs. ⁸ Total upcomings before and during oviposition period, the upcoming after the last lot of eggs being excluded.

N.B.—In the last three columns, nine females (Y down to E, inclusive) have each had one added to their scores because on the average they would have laid one further lot of eggs if allowed to live.

This table is designed to provide an approximate idea of the mean and range of performance of the female up to the end of her oviposition. Most females have completed oviposition when 70-100% of their eggs are laid. The first ten females (A down to M) were killed before they had laid 70% so naturally they contribute no data to the last four columns.

In short, the sample seems good enough to justify generalisations on female behaviour from the data in fig. 2. This fig. shows at once that there is a wide variety in behaviour. Some details have been extracted and set out separately in Tables IX, X & XI.

TABLE X.

The number of upcomings between spasms of oviposition.

Upcomings	1	2	3	4	5	6
Females \times occasions	20	9	1	1	1	1

TABLE XI.

The number of days spent underground during a spasm of oviposition.

Days	1	2	3	4	5	6	7	8
Females \times occasions ..	34	14	7	3	5	4	0	1

Egg-laying starts any time from a few hours after primary emergence up to at least 11 days later (and possibly 15 days later, see Note 4 of Table IX). This rather wide variation must be directly related to the state of the reproductive system at primary emergence: individuals with a fat-body score of 3 will take the longest and those with fat-body score 1 the shortest time to start oviposition (*cf.* Milne, 1959*b*). About half of the females (19 in 40) come up once only (primary emergence) before beginning to lay eggs; the remainder come up 2–8 times, *i.e.*, on 2–8 different days, spread over 2–11 consecutive days; on the average a female comes up twice before beginning to lay her eggs (fig. 2 & Table IX).

The female practically completes oviposition (*i.e.*, lays 70–100% of her fully formed eggs) by the end of 2–17 days after primary emergence, mean 8 days (Table IX). Confirmation of the earlier conclusion (Milne & Laughlin, 1956) that there is no regularity in the pattern of oviposition is given in fig. 2. A female may lay all her eggs in one lot or in several lots up to a maximum of four (or five, see female BB in fig. 2), the mean being about two lots (Table IX). She comes up 1–6 times between lots, mean 2 times (Table X). In laying any one lot, she stays underground 1–8 days, mean 2 days (Table XI).

Thus, before all her eggs are laid, a female has come to the sward surface and returned again underground from 1–10 times, mean 4 times (Table IX); and until at least 70 per cent. of her eggs are laid she always returns underground immediately after mating.

For proper appreciation of the experiment it should be added that a female in nature lays about 80 per cent. (0–100%) of her fully-formed eggs before dying and, in the majority of cases, completes her oviposition before entering Phase 2 (Milne, 1959*b*, and see later).

It is perhaps worth while repeating that the conditions of the experiment (soil, turf, temperature, humidity, light) were as nearly natural as possible. Moreover, the females were never disturbed while underground as was the case in all previous work (Raw, 1951; Milne & Laughlin, 1956), nor were they disturbed appreciably when on the turf surface. As a result of these considerations, more reliance can perhaps be placed in the findings as representing those occurring in the field.

Females undiscovered on the sward.

From the preceding four sections, it is clear that any female on bracken or trees with more than one-third of her eggs still unlaidd is there because at her most recent upcoming from the soil she was not discovered *on the sward* by a male in flying weather. The few such individuals which have not even begun to lay were tentatively called 'aberrants' (Milne, 1959b) but it is obviously better to lump them all together as 'undiscovered females.' These females form the bulk of the 'effective bee-liners' (see later). With Phase 1 overlapping Phase 2, one would expect the 'undiscovered females' to be derived mainly from the latter end of the female primary emergence curve because towards the end more and more males work on the bracken or trees and therefore fewer and fewer on the sward.

Contrast in male and female habits.

Unlike the female, the male generally never returns into the soil after primary emergence. Although in the first few days he disappears into the turf after activity (Milne, 1958), field investigation showed that he goes no deeper than the soil surface if cover is sufficient, as it usually is. His daily life consists in searching for and mating with females on the sward during the activity hours, then resting all night—first at the sward base, then on its surface (a small minority only) and, later, on the surrounding bracken and trees. He feeds in the early evening but not until he begins resting on bracken or trees, which is up to a week after his primary emergence (Milne, 1958). The female likewise does not feed until she takes to the bracken or trees, after all or most of her eggs are laid. Obviously both sexes sustain themselves entirely on their larval stores (fat-body) for the greater part of their adult life, measured from ecdysis. Here is the only similarity in behaviour. The great contrast is that in Phase 1 the male spends most of his time above ground, while the female spends practically all hers below—coming up only very briefly now and then to mate.

Behaviour in phase 2.*Swarming.*

Previous writers have remarked that garden chafers 'congregate' on bracken, bushes and trees "later in the season," again without attempting analysis of the behaviour (Milne, 1958). The 'congregation' is in fact just a continuation of swarming, only the swarming site has now shifted from the grass sward to the proximate edge of its surrounds. The trees and bushes concerned are deciduous. The present writer never found garden chafers on a pure conifer plantation bordering an infested sward; and where deciduous and conifer trees mingled in a border, only deciduous trees were occupied. The reason probably is that conifer needles are unpalatable.

The swarming takes place among the upper fronds of bracken and among the outer leaves from top to bottom of trees (up to 60 ft. high). Here it has much the same characteristics as on the grass sward except that more females are present, they fly more and their mating is always in full view. The males still alternate between (1) weaving in feverish flight close to the general surface of the vegetation and (2) alighting to run over it. In general, the females are still much less energetic, spending much more time on the fronds (or leaves) than in the air. When a female does fly, it is not a feverish weaving among the fronds but rather a hop from one frond to another or, in a minority of individuals, the bullet-like departure of the 'bee-liner.'

'Bee-lining.'

'Bee-liners' have been mentioned frequently but not explained fully in earlier papers (Milne, 1958, 1959a, b). The term 'bee-liner' was coined to distinguish

certain individuals peculiar for their manner of flight. Bee-liners were studied at two sites already described (Milne, 1958), *viz.*, Upper High House Field, Buttermere and Target Field, Rydal.

Throughout the season, the characteristic flight of the mass of beetles is a comparatively restricted random weaving within a limited site (either the grass sward, or its surrounds). After Phase 2 starts, however, one sees some individuals performing more or less straight flights from one site to another. Thus, if one stands near bracken or a tree (or hedge) in flying weather, every now and then one notes the arrival of an individual flying in from the sward to alight among the weaving throng on the upper fronds or outer leaves. These individuals, the incomers, are males and females joining or rejoining phase-2 activity. At the same time one also notes some individuals emerging from the throng on bracken or tree to fly out over the grass sward. These latter, the outgoers, are of considerable interest. Between 25 and 50 per cent. of females present on bracken and trees still have some eggs unlaidd (Milne, 1959*b*, Tables XI & XIV). Were these the outgoers, and if so where did they deposit those eggs? Only the following-up of individual outgoers could tell.

In time it became clear that there were two kinds of outgoing behaviour. Some individuals flew out in a comparatively leisurely fashion, curving to one side or the other, or, in longer flights, from side to side; these never climbed in flight but kept low and soon descended on the grass sward nearby, sometimes only 2 yards away, generally less than 10 or 20 yards, and never more than about 50. Others, in sharp contrast, shot out straight and fast—almost bullet-like; these always climbed at a greater or lesser angle for a start so that they flew at higher levels and descended either much farther out on the home sward or outside the study field altogether. The latter were called 'bee-liners' because of their swift straight flight so reminiscent of a homing bee. On capture, bee-liners proved invariably to be females, while the individuals exhibiting the shorter, lower, more leisurely, arc-ing flight were always males. The contrast in speed, directness and height of outgoing flight is so sharp between females and males that one can reliably sex the outgoer in the air many yards away, as was confirmed over and over again at subsequent capture. In four years, a male was seen behaving like a female and a female like a male only once in each case.

During the period when Phases 1 and 2 overlap, the outgoing male joins in the now waning activity on the grass, this sometimes entailing one or more additional low flights of 10 or 20 yards after the first landing. From the end of Phase 1, however, he wastes little time looking for what is no longer on the sward (a swarm) or for the now rare female there and usually returns to the bracken or trees following a little run around the point where he landed from his outgoing. After the end of Phase 1 also, far fewer males than females fly out any distance from bracken or trees. Thus, on four occasions, when sex ratio on bracken was approximately unity, the female:male ratio among outgoing beetles ranged from 6:1 to 19:1.

The method of studying bee-liners was to stand on watch near the edge of the bracken or near a tree and chase after any individual that shot out. Including those captured for dissection (Milne, 1959*b*), the behaviour of several hundreds of individual bee-liners was observed in whole or in part during the five seasons 1949–1953. More often than not the chase had to be abandoned when either the female vanished against a dark background, or climbed out of sight (trees 100 feet high were cleared) or travelled so far that the observer either lost his breath or was halted by wall or fence (on a warm day the female soon outstrips the fleetest human being). Nevertheless, complete details from take-off to landing were obtained for just over 100 individuals. The findings are summarised below.

A female gives little or no warning that she is about to do a bee-line. The following is a description of the typical procedure on bracken about 2.5 feet tall.

The sun must be shining. The female is resting immobile on a frond while males weave around, alternately flying and settling. She starts to walk about on the frond. She arrives at the tip, pauses, opens her wings, gives them a preliminary short flutter, then abruptly rises vertically upwards, usually to a height of 3-5 feet (max. 20 ft.), above the bracken tips and the milling throng. She hovers a second or two, darts to the bracken edge (without losing height), seems to pause an instant and rise a little more, then instantly shoots out over the grass sward, climbing straight as an arrow. The angle of climb is generally 10-20 degrees and may be increased later to surmount obstacles such as trees. (Note: a male outgoer merely detaches himself from the throng, without rising above it and he does not climb thereafter.)

Bee-liners shoot off at all heights from trees. At eye-level, the behaviour is the same as on bracken; higher up, the initial vertical rise is understandably curtailed or absent. The angle of climb also seems to be less than on bracken and possibly decreases with height of take-off.

In calm weather, bee-liners shoot off to all points of the compass; in a moderate breeze they go downwind.

The initial angle of climb largely determines how far a bee-liner travels before landing; the steeper the angle the farther she goes. For a given angle she will naturally go farther down a hill-side than up. Should the sun disappear behind a cloud, she immediately lands. This was usually the cause of short bee-line flights (3-40 yd.). Normally the bee-liner flies 50 to 300 yards or more. Of a total of 67 bee-liners pursued by one of the observers, 17 landed within 100 yards of the bracken edge, 20 flew at least 100 yards (still in flight when lost), 17 flew at least 100-200 yards, 12 at least 200-300 yards, and 1 at least 300 yards (when it was still going strong). This last was the limit of our achievement in pursuit on a cool sunny day; on a hot sunny day, with flying speed consequently faster, the beetle was beyond visual range by the time it had flown 100-150 yards.

The great majority of bee-liners fly beyond the area where they lived as larvae and rather more than half of them leave the field (containing that area) altogether. The maximum distance they travel was not ascertained, but when sunshine was intermittent (causing them to land willy-nilly) they were found quite plentifully on the pavements right through the town of Ambleside. Thus, on one collecting walk, 10 females were picked up between the town boundary and half way in; and 7 from there to the town centre, which is between quarter and half a mile from the nearest larval habitat. (As would be expected, male beetles were never found on the pavements.)

Behaviour *after* landing was observed in bee-lining females which touched down within 100 or 150 yards from bracken or trees, *i.e.*, on the area of sward from which they originated. Although 40 such cases were studied, complete histories were obtained in less than half, for a reason which will appear below.

On landing, some females, after the briefest random walk-around (a few seconds, within a diameter of 2 or 3 in.) on the sward surface, dig themselves into the soil immediately and stay down. Others walk around for a few seconds or minutes then fly (in bee-line fashion) to another point from 2 to 200 yards away or more (those flying farthest were often lost, hence the incomplete histories mentioned above); this may be repeated one to four times (maximum observed), a female sometimes even going down to the soil surface and coming up again before she finally arrives at a site where she is content to burrow into the soil and remain there. The following is a typical instance of the latter behaviour: The female, bee-lining from bracken, alighted on the sward about 60 yards out. There she walked around and up and down stalks and stems for about 5 minutes. Then suddenly she took wing, flying another 40 yards (in bee-line fashion), and after a few seconds of walking burrowed down to the bottom of the mat. Almost immediately she came up again, walked around for 3 or 4 minutes, then entered

the soil about 18 inches from her second landing point. As in some other cases, the spot was marked with a wire peg and the female recovered from the soil in the evening. She contained 4 eggs and no fat-body.

Behaviour after the first or only landing could be the result of discrimination as to the type of sward and/or soil for oviposition. In every case where *immediate* entry of the soil occurred at the first landing point, such landing was made on the uninjured edge of a patch of sward damage previously caused by larvae of the generation to which the bee-liner herself belonged. Such a situation is eminently suitable for development of the garden chafer, as sampling has shown (see later paper), and the bee-lining female may be able to 'recognise' the situation or its suitability at once. At any rate the reaction is still immediate if the bee-liner alights on the edge of a damaged patch not at the first landing but at second or subsequent landings, as the following typical example shows: This particular female shot out from the bracken and landed about 50 yards out on a large undamaged area. She made four further flights (2-30 yd. each) separated by walks-around, the first three being within the same undamaged area, and at the second hop dug a quarter of an inch into the soil but came up again. The fourth hop took her to the edge of a damaged patch where she entered the soil almost immediately and stayed down. Recovered later, she was found to have 6 eggs and no fat-body. The whole procedure, from leaving the bracken until final disappearance into the soil took 7 minutes. Of course, many females did finally enter the soil and stay down where there was no damaged patch in the near vicinity, but they made their 'decision' less quickly. In such cases the observer could see no obvious sward or soil difference between the point or points rejected and the point finally selected for entry.

As indicated earlier, between 50 and 75 per cent. of females on bracken contain neither eggs nor fat-body. The vast majority of these spent females do not leave the bracken but a few do bee-line off, and, in fact, a previous paper (Milne, 1959b, Table XV) showed them as comprising about 10 per cent. of all bee-liners. It was right to include them among the bee-liners because they do shoot off fairly straight and fast from bracken and trees. But the initial bee-line never takes them beyond the home sward, indeed seldom far across it, and behaviour afterwards is not typical of bee-liners in that urgency ceases after landing. Thus, the spent female's movement on the sward is comparatively slow and may be punctuated by feeding; her subsequent flights are not in bee-line fashion but in leisurely loops; she does not attempt to go down into the sward until an hour or two has passed and if she digs into the soil she goes no deeper than is necessary just to bury herself. One typical example will suffice: This female flew out from the bracken at 1330 hr., alighted about 20 yards out and walked slowly around on the sward surface. At 1340 hr. she flew 30 yards, low and veering across the light wind. She then walked around, stopping frequently to eat petals of wild thyme flowers in her path, until 1520 hr. when she dug just below the surface of the soil (0.5 in.).

The important facts about bee-liners then are: (1) they are all females; (2) they are a minority among females; (3) about 90 per cent. of them have one or more eggs still unaid; (4) about half of those containing eggs fly clear out of their home field, usually in one hop, sometimes in two or more hops, the maximum distance before settling for oviposition being at least greater than quarter of a mile and possibly half a mile or more; (5) they seem to exercise some discrimination as to the type of sward and/or soil for this, their final, oviposition.

Effective bee-liners.

Effective bee-liners are those that actually lay eggs after quitting bracken, hedge or tree. Neither their numbers nor their oviposition after bee-lining can be measured directly in the field. These can be roughly estimated indirectly,

however, by manipulating various sample data (as below). It will be noted that some of the sample statistics are used as if they were actual population parameters. In these cases the samples were very large (500-1,500 individuals) and the (consequently) very small sampling errors can be ignored without detriment to present purposes. With smaller samples, sampling error is taken into account by using 5 per cent. fiducial limits.

It will be recalled that the average female manufactures and matures a total of 16 eggs, of which she lays 13, leaving 3 still unlaidd at death (Milne & Laughlin, 1956; Milne, 1959b). Throughout Phase 2 in five seasons, females, collected at

TABLE XII.

Distribution of eggs in (a) females on bracken and trees (potential bee-liners), (b) females shooting off bracken and trees (*actual bee-liners in general*) and (c) females crawling on pavements near the centre of Ambleside (*actual long-distance bee-liners*).

Eggs	Numbers of females		
	(a)	(b)	(c)
1	220	5	8
2	110	3	1
3	75	—	1
4	63	3	—
5	38	2	2
6	28	2	1
7	19	4	2
8	12	5	1
9	19	2	2
10	14	5	1
11	12	2	2
12	6	5	1
13	8	2	3
14	6	7	2
15	4	4	3
16*	39*	15*	1
17	6	3	1
18	3	2	—
19	3	—	—
20	2	3	—
21	2	1	—
22	1	3	—
23	1	2	—
24	—	—	—
25	1	—	—
26	1	—	—
27	—	—	—
28	—	1	—
Mean eggs per female ..	4.72	12.28	8.06
Standard error	0.19	0.68	0.98

Complete data for 1949-1953 except that females containing neither eggs nor fat-body are excluded since they could not be effective bee-liners.

* A female lays no eggs until her fat-body is entirely consumed. Females with any fat-body remaining were all classed as containing 16 eggs since that is the average total production. There were 36 such females in (a), 12 in (b) and none in (c).

random from bracken and trees, were kept in small groups either in oviposition jars or in cages permitting oviposition in the natural turf outdoors. Results were the same in jars and cages. Taking all the data together, 519 females laid 994 eggs before dying, mean 2 per female. Thus, since the average female lays a total of 13 eggs (see above), about 15 per cent. of the total oviposition of a population is laid by bee-liners. Hence, the number of effective bee-liners cannot be less than 15 per cent. of the female population. In fact, the number is certainly greater than 15 per cent. because only a little over 1 per cent. of females arrive on bracken and trees before beginning to lay (Milne, 1959b). On the other hand, since only 45 (or 26.2%) in a sample of 172 females *at their first arrival* on bracken had any eggs left (Milne, 1959b, Table XI), the number is unlikely to be more than 33 per cent. (upper fiducial limit on the 0.05 probability). In fact the number is certainly less than 33 per cent. as the following shows (see Table XII): Among *potential* effective bee-liners (those females, on bracken or trees, containing one egg or more) the mean egg-content is not more than 5. But the corresponding mean content of *actual* bee-liners in general is 11.13 eggs (5% fiducial limits from 12.28 ± 0.68) which is very considerably higher. Thus, not all the potential bee-liners do bee-line, and obviously the failures are mainly among those in the lower end of the range of egg-content. Clearly the number of effective bee-liners is certainly more than 15 per cent. and certainly less than 33 per cent. of the female population. These limits can be narrowed more precisely as follows.

The average effective bee-liner must lay 8–10 eggs (*i.e.*, 11–13, less 3 unladen at death) after leaving bracken, hedge or tree. Hence, the 994 eggs would be laid by 99–124 (*i.e.*, $994/10$ – $994/8$) of the 519 individuals taken from bracken and trees (see above). In other words, effective bee-liners comprise 19–24 per cent. of the female population and on the average lay 8–10 eggs each, range being from one egg up to the total eggs produced and laid.

Finally, it will be noted (Table XII) that 'long-distance' bee-liners have an average egg-content of 8.06 ± 0.98 as compared with 12.28 ± 0.68 ($P = <0.001$) among bee-liners in general. This suggests that bee-liners with more eggs to lay travel shorter distances—probably those with most eggs do not leave their home field.

Contrast in male and female habits.

The male leads the same kind of life in both Phases. The female, on the other hand, changes from a largely underground life in Phase 1 to a largely above-ground life in Phase 2. Apart from the greater bustling of males, habits of the sexes are largely similar in Phase 2, *viz.*, the active hours (max. 0800–1600 hr. G.M.T.) are spent mostly in perambulating, flying, mating and prolonged post-coitus clasping, the remainder of the day in feeding (early evening) and resting (night)—all on the bracken or trees. The main contrasts are: (a) females are arriving on bracken or trees until the end of Phase 2 while males have all arrived by the end of Phase 1; (b) female departures (outgoing flights) continue throughout Phase 2 while male departures virtually cease by the end of Phase 1; (c) female departures are in bee-line fashion while male departures are not.

End of life.

It will be remembered that activity counts were made daily on the grass sward at fixed stations (Milne, 1958). In 1949 and 1950 these stations were also examined every evening and all dead beetles collected. Corpses were sufficiently numerous to be noticeable 15 and 16 days, respectively, after the beginning of the flight season. This confirms the former conclusion (Milne & Laughlin, 1956; Milne, 1956, 1959a) that in the field an average adult lives about a fortnight after

primary emergence on the sward. From the collections it was estimated that less than 2 per cent. of the beetle population died naturally (*i.e.*, of old age) on the surface of the sward and at the rate of 5 males to every female. Obviously, nearly all males (excluding those eaten on the sward by birds) die on the bracken and trees (where birds pay little or no attention to them), and fall to the ground below. A majority of females does likewise, but, as was revealed in sampling for eggs, many die in the soil under the grass sward after completing oviposition.

Concluding discussion on the flight season.

The features of the flight season have now been described and analysed at length in this and the preceding three papers. The following is a brief concluding discussion of the season and its ecological implications.

The explanation of its grosser features—the roughly equal and half-overlapping Phases 1 (on the sward) and 2 (on the surrounding bracken and trees), together lasting about 26 days (in a homogeneous population)—should now be clear. These features obviously result from (a) primary emergences occurring over the first 12–13 days of the season and (b) the average individual leaving the sward for the surrounds about half way through its 13–14 day life after primary emergence. The less obvious features—sex proportions and female reproductive state among beetles present in the swarms of Phase 1 and of Phase 2 and in the traffic to and from these swarms (including ‘undiscovered’ and ‘bee-lining’ females)—have likewise been rationalised in terms of (a) and (b) above, together with (c) slight male precedence in primary emergence, (d) variation in reproductive development of females at primary emergence and (e) wide differences in habits and behaviour of the sexes. This need not be elaborated again. One major puzzle remains. Why does the garden chafer leave the grass sward to spend the latter half of its life on the bracken or trees?

The adult garden chafer does not start feeding until it goes to the bracken or trees, and there it partakes of the fronds or leaves. But “since the beetle readily eats various sward constituents (preferring, for instance, salad burnet (*Poterium sanguisorba*) to bracken in the oviposition jar), migration to bracken, hedges and trees (Phase 2) is not caused by the need for food” (Milne, 1959b). The prime cause has not been found. It is perhaps worth remarking, however, that migration concentrates the population. Garden chafers congregate mostly on the proximate edges of the bracken, etc., and there the density necessarily becomes greater than on the wide expanse of grass. This concentration of numbers, and hence of activity, is perhaps needed to ‘trigger off’ the bee-lining instinct in females which have not completed oviposition, but that would be a result of migration not the cause of it. The feeding does not enable any more eggs to be manufactured (Milne & Laughlin, 1956), nor possibly any more sperm (this not investigated). But it must provide the energy for all phase-2 activity of males and females, including bee-line flights among the latter, because the beetles have no fat-body left when they take to the bracken and trees.

From the economic viewpoint the ecological questions that interest us most are spatial distribution and time distribution (growth, fluctuation and control), of numbers of the garden chafer. These distributions must be fundamentally influenced by certain aspects of male and female behaviour in the flight season.

Spatial distribution.

As has been shown, the swarming of males and the reactions of females following upon male clasping in Phase 1 result in 85 per cent. of all eggs being deposited in precisely the same places as were inhabited by their parents. This must tend very strongly to maintain existing patchiness of distribution. New patches arise from the remaining 15 per cent. of eggs, these being laid by bee-liners, some in new parts of the home field, others in new fields adjacent.

Successful establishment of a new patch (colony) depends primarily, of course, on choice of a favourable oviposition site, and bee-liners seem to exercise some power of discrimination thereunto. Given a favourable site, the colony, although it may start with only a small number of eggs, has a better chance of persisting and growing in extent simply because male and female behaviour dictates that descendants will tend to lay most of their eggs in the same site every year.

Time distribution.

Male swarming and female reactions to male clasping in Phase 1 have both advantages and disadvantages for the population of the garden chafer in any given area. On the one hand, this joint behaviour (1) reduces the exposure of gravid females to bird predation and (2) provides for most eggs being laid in places where their parents lived successfully; on the other, it (1) increases the exposure of males to bird predation (the droppings of starlings and visiting flocks of seagulls are often composed almost entirely of fragmentary male exoskeletons) and (2) ultimately lessens the favourability of some of these places by changing the composition of the sward through over-population. Other things being equal, however, such joint behaviour should cause faster population growth and, up to a point, a higher average population level through time than any less restricted behaviour would do.

'Undiscovered females', those taking all or most of their eggs away from their birthplace (see pp. 357 and 367), are the result of insufficient density of searching males in warm sunny weather. It follows that proportionately more females are liable to be 'undiscovered' in a low than a high population. Hence, a new colony, or an older population which has decreased, should have more chance of increasing in numbers if weather in Phase 1 of succeeding seasons is mainly warm bright-overcast. Such weather permits females to walk and males to run in search of them, but it prevents females from flying and so becoming 'undiscovered females.' However, skies are seldom if ever consistently overcast throughout Phase 1 and some females are 'undiscovered' even in the highest populations. Therefore it is probably right to conclude that sunny weather, by its effect on behaviour of temporarily undiscovered females, always helps to reduce multiplication below the potential in any particular place but more so the lower the population.

All these ecological matters will be referred to again, and enlarged upon where necessary, in following papers on spatial and time distributions and on sward damage. Enough has been said now to indicate the ecological importance of the flight season.

Summary.

This part of the study of the garden chafer, *Phyllopertha horticola* (L.), in the English Lake District deals with behaviour of the adult males and females, and completes the appraisal of the flight season.

The outstanding features of the flight season are two roughly equal and half-overlapping phases of mass activity: Phase 1, swarming over the grass sward, followed by Phase 2, swarming on the surrounding bracken, hedges and trees.

Behaviour in Phase 1.—Swarming is essentially a male activity. It is a feverish concentration of males alternately weaving in flight close over the ground and alighting to run around in search of females emerging. Females do not take part in the weaving flight; they perambulate slowly with occasional pauses and, being heavily outnumbered on the sward, tend to be quickly immobilised by pairing. Swarming is confined to the areas of sward from which the beetles emerge. Mechanisms involved in the siting and coherence of swarms are suggested.

Both males and females change direction frequently and randomly while moving upon the sward. Pairing depends almost entirely on the chance physical encounters (collisions) arising from this activity.

In most cases a female is discovered by a male within one minute of starting to walk from her emergence point. (If not discovered by about four minutes (average) in hot sunny weather, she begins to fly (no weaving) and may appear on bracken or trees before beginning or, more often, before completing oviposition. Such 'undiscovered' females form the bulk of effective 'bee-liners' in Phase 2.)

When a male discovers a female on the sward, he immediately clasps her. At primary emergence, and at any subsequent emergence before 70–100 per cent. of her eggs are laid, the female reacts at once by descending vertically into the sward where mating (average 12 min. duration) takes place in concealment. This finished, she 'shrugs' the male off and continues vertically downwards to burrow into the soil. The male, on the other hand, quickly ascends to the surface and at once begins searching for another female. On the average the straight-line distance between the emergence point and soil re-entry point of a female (excluding the 'undiscovered' minority) is little more than 7 inches (observed range 0–29 in.). Hence, most of a typical female's eggs are deposited in practically the same place as she herself lived her larval existence.

On emerging after 70–100 per cent. of her eggs are laid, the female behaves quite differently. She mates unconcealed on the sward surface and, coition completed (average again 12 min.), walks around with the male on her back until he leaves of his own accord 5–30 minutes later. Then, after a further 10–20 minutes of walking and resting, she flies to the nearest bracken or trees (thus entering Phase 2) where she mates again, and feeds—for the first time as an adult—in the early evening.

In Phase 1, a female may come up (emerge on the sward surface to mate) and then go down (re-enter the soil—not always to oviposit) several times, but never more than once on any day. Egg-laying starts any time from a few hours after primary emergence up to 15 days later. Before beginning oviposition a female comes up 1–8 times, average twice (including primary emergence). She completes oviposition by the end of 2–17 days after primary emergence, average 8 days. The oviposition pattern is very varied and irregular. Her eggs are deposited in 1–4 lots, average 2. Between lots she comes up 1–6 times, average twice. In laying any one lot she stays underground 1–8 days, average 2. Before completing oviposition, she has come up and gone down 1–10 times, average 4. She lays about 80 per cent. (0–100%) of her fully formed eggs before dying, and, in the majority of cases, completes her oviposition before entering Phase 2.

The male generally never returns into the soil after primary emergence. His daily life consists in searching for females as they come up around midday, and resting during the remainder of the 24 hours—first at the base of the sward and later on the surrounding bracken or trees. He feeds in the early evening but not until he begins resting on bracken or trees, which is up to a week after his primary emergence. Like the female he subsists on larval stores (fat-body) for the greater part of adult life, measured from ecdysis. The great contrast is that the male spends most of his time above ground, while the female spends practically all hers below, in Phase 1.

Behaviour in Phase 2.—The swarming on bracken or trees is essentially the same as on the grass sward. The only differences are that now more females are present, they fly more (though never weaving) and their mating is always in full view (on fronds or leaves).

Throughout Phase 2, some individuals fly away from the swarm on bracken or trees. Those with the low, leisurely, arc-ing flight are all males and all land nearby on the home sward. Those with the high, bullet-like flight, the so-called

'bee-liners,' are all females and are a minority among females. About 90 per cent. of bee-liners have one or more eggs still unlaidd and about half of them fly clear out of their home field, the maximum distance being at least greater than quarter of a mile; they seem to exercise some discrimination as to type of sward and/or soil for completing oviposition. Effective bee-liners, those that actually oviposit, comprise 19-24 per cent. of all females; on the average they lay 8-10 eggs each.

Apart from the greater male activity, habits of the sexes are largely similar in Phase 2, *viz.*, the active hours are spent mostly in perambulating, flying, mating and prolonged post-coitus clasping, the remainder of the day in feeding (early evening) and resting (night)—all on bracken or trees. The main contrasts are: Females are arriving on bracken or trees up to the end of Phase 2, males have all arrived by the end of Phase 1; female departures (outgoing flights) continue throughout Phase 2, male departures virtually cease by the end of Phase 1; female departures are in bee-line fashion, male departures are not.

The average adult lives about a fortnight after primary emergence on the sward. Nearly all males (excluding those eaten by birds) die on the bracken and trees. The majority of females does likewise but many die in the soil after completing oviposition.

Conclusions on the flight season.—The grosser features—the two overlapping Phases lasting about 26 days overall with a homogeneous population—result from (a) primary emergences occurring over the first 12-13 days of the season and (b) the average individual leaving the sward for the surrounding bracken or trees about half way through its 13-14 day life after primary emergence. Other features—sex proportions and female reproductive state among beetles present in the swarms of Phase 1 and of Phase 2, and in the traffic to and from these swarms—result from (a) and (b) together with (c) slight male precedence in primary emergence, (d) variation in reproductive development of females at primary emergence and (e) wide differences in habits and behaviour of the sexes. The flight season is important ecologically because certain aspects of behaviour at that time (male swarming, female reactions to male clasping and to delay of clasping, in Phase 1; bee-lining in Phase 2) affect spatial and time distribution of numbers of the garden chafer.

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References.

- GRAY, R. A. H., PEET, W. V. & ROGERSON, J. P. (1947). Observations on the chafer grub problem in the Lake District.—*Bull. ent. Res.* **37** pp. 455-468.
- MILNE, A. (1956). Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). II. The cycle from egg to adult in the field.—*Bull. ent. Res.* **47** pp. 23-42.
- MILNE, A. (1958). Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). IV. The flight season: introduction, and general aspects.—*Bull. ent. Res.* **49** pp. 685-699.
- MILNE, A. (1959a). Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). V. The flight season: sex proportions.—*Bull. ent. Res.* **50** pp. 39-52.

- MILNE, A. (1959b). Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). VI. The flight season: reproductive state of females.—*Bull. ent. Res.* **50** pp. 467–486.
- MILNE, A. & LAUGHLIN, R. (1956). Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). I. The adult and egg production.—*Bull. ent. Res.* **47** pp. 7–22.
- RAW, F. (1951). The ecology of the garden chafer, *Phyllopertha horticola* (L.) with preliminary observations on control measures.—*Bull. ent. Res.* **42** pp. 605–646.
- RITTERSHAUS, K. (1927). Studien zur Morphologie und Biologie von *Phyllopertha horticola* L. und *Anomala aenea* Geer (Coleopt.).—*Z. Morph. Ökol. Tiere* **8** pp. 271–408.

APPENDIX.

Miscellaneous matters connected with behaviour.

Now that mass and individual behaviour has been fully described and analysed, certain remarks in earlier parts of this series can be explained or justified.

Part I (Milne & Laughlin, 1956).

Page 21. "As it happens (see later paper), the jam-jar environment is less artificial for the female than one might expect—at least for the first half of her life after primary emergence above ground, but for the male the conditions are exceedingly unnatural." Facts in the present paper amply justify this statement. Until most of her eggs are laid, the average female functions *naturally* in a universe which is smaller vertically and only a little larger horizontally than the jam-jar.

Part II (Milne, 1956).

Page 41. The last larva to complete feeding is about 41 days after the first larva to do so, yet the entire population emerges from the pupal stage within about 8 days only. "This (time-contraction)," it was said, "facilitates mating." Obviously it must facilitate mating since females are more readily found the more males there are above ground, and at any moment there would be more males available when ecdyses are confined within 8 days than when extended over 41 days simply because the average male has only 13 days above ground.

Part IV (Milne, 1958).

Page 686. "Plainly the (previously) published information on the flight season is incomplete and rather vague even where it contains no contradiction; in some respects it is also erroneous (see later)." Dr. F. Raw wishes it to be pointed out that the third line in the second paragraph of p. 685 should read: "With (a, b, c, d) or without (c, d) a prelude of small numbers . . ." This apart, the above general statement is justified by comparison of the said information with Parts IV to VII of the present series. There is little to be gained, however, by going into a detailed comparison here.

Part V (Milne, 1959a).

Page 44. In the 1951 field experiment on primary emergence, "males [*i.e.*, male pupae] were introduced into one square, females into the other . . ." The reason for segregation is now seen to be that, with no males present, females

remain longer on the surface and hence their primary emergence is not missed if observation has to be suspended for a few minutes.

Page 47. The very low ratio of females to males seen above ground in Phase 1 is not only due to the fact that "unlike the male, the female is not present on the sward every day after her primary emergence." As has now been shown, it is also partly due to the extreme shortness of her stay on the surface whenever she does come above ground.

Page 49. The proportion of unpaired females seen on the sward at the daily peak of activity increases as Phase 1 proceeds. This is partly the outcome of the accompanying fall in the relative number of males, "which means fewer searching for each female so that she is less readily found. As will be shown in a later paper . . . it is also partly due to a striking change in the mating behaviour of the female as she ages." This change, as now described, results in the female permitting the male to clasp her very much longer and in her not returning into the soil when the male leaves, both of which in effect still further reduce the relative number of males searching for each female.

A THERMAL PREFERENCE METHOD OF BIOASSAY OF THE TOXICITY OF INSECTICIDAL FILMS TO HOUSE-FLIES.

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P.L.

The method described in this paper was developed to compare the value of insecticidal deposits formed by spraying DDT or other insecticides formulated in several different ways, using house-flies, *Musca domestica* L., as the test species. The requirements were that the method should be sensitive enough to distinguish between deposits differing in toxicity by a factor of 1.5; that it should operate with an exposure time of about five minutes; and that the insects should be crawling over the deposit during the whole exposure period. Insects that cannot crawl on vertical glass surfaces and are reluctant to fly present no difficulty, but some way must be found of persuading such insects as house-flies to remain on the test surface.

In the past, this difficulty has been overcome in one of three ways:—

(a) The insects are enclosed in a space, part of the walls of which constitute the test surface. The insects have a free choice between treated and untreated surfaces when they settle.

(b) All the surfaces enclosing the insects are treated with insecticide, so that the insects are always on a treated surface except when they are flying.

(c) A single flat test surface is used, and the insects are in some way discouraged from crawling on the other surfaces and from flying.

The methods under (a) are used when field conditions are to be simulated, so that a deposit that is repellent will appear to be less effective than one that does not repel. It is therefore not suitable for simple comparisons of toxicity. Methods in the category under (b) above are only suitable for use with one particular type of surface, and comparisons between different types are not possible. Furthermore, the dose received by an insect depends on whether the surface upon which it crawls is vertical or horizontal.

For methods under category (c) above, a number of devices have been used to discourage insects from resting on untreated surfaces. With mosquitos confined to a rough surface by means of an inverted Perspex funnel, the tendency for them to rest on the polished Perspex is small, and no special device is necessary (Hadaway & Barlow, 1951). House-flies may be discouraged from walking on glass by smearing it with an involatile oil (Busvine, 1957) or dusting it with powder. These methods are not entirely successful, and they may contaminate the flies with a foreign substance. Some insects will remain on a flat surface when covered with a lid which meets the surface at an acute angle, *e.g.*, an inverted clock-glass, but they often tend to rest in the angle between the surface and the lid instead of walking about during the test.

A method has been described (Gratwick, 1957) in which blowflies, *Phormia terraenovae* R.-D., are confined on the test surface in a space that allows them to crawl about, but that is too shallow to allow them to turn over or to fly. This method was adapted to house-flies, and studied in some detail (R. A. Harrison, *priv. comm.*) but it had two defects:—

(1) It was applicable only to smooth surfaces.

(2) The results were seriously influenced by the size of the gap between the test surface and the ceiling of the chamber; variations in the size of fly from one

culture to another called for different gaps. Moreover, the flies were held on the deposit in an unnatural attitude, with their tarsi pressed flat on the surface and sometimes with their abdomens touching it. An attempt was therefore made to find a method of keeping flies on a test surface without these disadvantages.

A number of unsuccessful methods will be mentioned briefly. A bright light shining upwards through a glass plate tends to attract flies, but there are always a few individuals that fail to respond. A cylinder made of bent wire, rotating just above the test surface, repelled the flies for a short time, but eventually they ran towards it and escaped through the wires. A transparent plastic cylinder marked with black strips and rotating was rather more successful, but some flies jumped on to it and, once there, they remained on it. It has been reported that some insects cannot crawl on surfaces coated with polytetrafluoroethylene, because the static coefficient of friction is too small. A pilot experiment showed that, though the flies could not move about as freely on this material as on glass, they were able to walk on it, even when the surface was vertical.

The method finally adopted depends on warming the test surface to about 30°C. and confining the flies within a circular chamber the walls of which are kept cool. The flies walk about freely during the exposure period, but they seem able to sense the temperature gradient, for they remain on the preferred warm surface and rarely go near enough to the cold chamber wall to touch it. This method can be used with deposits on most types of surface, including large leaves, which are fixed to glass plates by adhesive tape before spraying.

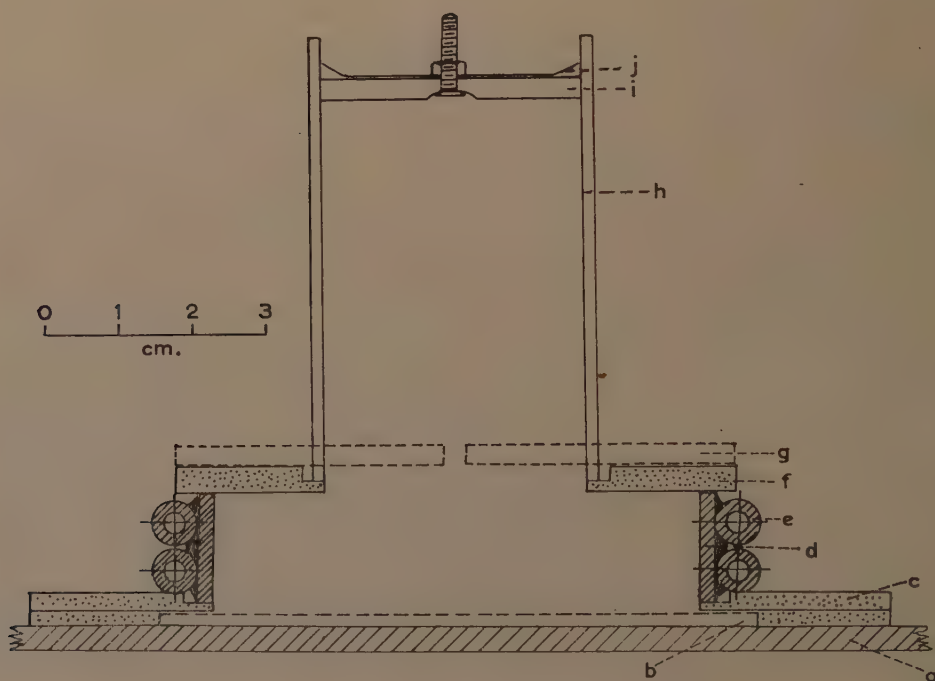


Fig. 1.—Apparatus used to confine house-flies to the test surface during exposure: a, hot-plate; b, slot for glass plate carrying deposit; c, Perspex plate; d, cold cylinder; e, cooling coil; f, Perspex plate with round recessed hole; g, position of Perspex lid; h, glass tube; i, Perspex plunger; j, friction spring.

Apparatus and methods.

A large metal plate (figs. 1 & 2) forms the lid of a box that contains an electric-light bulb controlled by a thermostat, set so that a thermometer laid on the plate, with its bulb covered with cotton-wool, reads 33°C. The glass plates carrying the deposits to be tested are laid on the metal plate and allowed to reach thermal equilibrium. The test chamber consists of a short section of brass tubing 6.5 cm. in internal diameter and 1.7 cm. deep. Thin copper tubing is wound



Fig. 2.—Apparatus used to confine house-flies to the test surface during exposure, with glass tube and Perspex plunger in position for introducing insects into the test chamber.

round the outside and soldered to the brass; ice-water circulating through the copper tubing keeps the brass ring cool. The brass ring stands in a recess over a hole in a Perspex plate, which is raised from the metal plate by two distance-pieces, leaving a space into which an insecticide-treated glass plate can be slid to form the floor of the chamber. The roof of the chamber is a piece of Perspex with a hole in it.

The insects for test are counted into glass tubes, each 6.5 cm. long by 3.7 cm. diameter, having one end closed with gauze and the other with a Perspex plunger bearing a strip of spring metal to provide friction. The plunger is used to displace the flies from the tube when required; a similar method of introducing insects into a test chamber is described by Derbenova-Ukhova (1952, pp. 242–248).

The culture of house-flies is chilled, and batches of ten females are put into the tubes. They are allowed a period of about two hours to recover from the chilling.

To prepare the apparatus for use, the hot-plate is switched on and allowed to warm up. A siphon is established through the cooling coil, drawing water from a raised bucket containing ice-cubes and water. The temperature of the effluent is normally 10°C. A clean glass plate is first slid into the chamber. The gauze on one of the tubes of flies is removed and replaced by a glass plate. The tube is then inverted and slid from the glass plate into the recess round the hole in the lid of the test chamber. The Perspex plunger is pushed down, causing the flies to enter the chamber. The tube is then removed and the hole in the chamber lid covered by a thin piece of Perspex. A flat-bottomed dish containing ice is placed on top, to discourage flies from resting on the underside of the lid.

The glass plate bearing the deposit is placed on the metal hot-plate, and is left there for five minutes, long enough to reach thermal equilibrium. When the flies have been introduced into the chamber, the warmed treated plate is slid in, pushing out the clean glass plate. After the exposure the clean plate is again slid in, the flies are anaesthetised with carbon dioxide and transferred to a retaining tube, in which they are fed with sucrose solution on a cotton plug. The retaining tubes are kept at 20°C. The number of dead is counted after 24 hours.

Studies have been made on the comparative toxicity of deposits of suspensions, emulsions and solutions of DDT and some of the data are given below to illustrate the performance.

The deposits were produced by spraying glass plates in a Potter tower (Potter, 1952). The suspension consisted of needles of DDT 60 μ long, suspended in an aqueous solution of wetting agent (McIntosh, 1947). The emulsion was prepared by mixing 8 ml. of a 25 per cent. w/v solution of DDT in xylene with 1 ml. of Agral LN* and stirring mechanically while slowly adding 100 ml. of water. The resulting emulsion was diluted to 1 litre with water, giving a concentration of 0.2 per cent. DDT; other dilutions were made from this by adding 0.1 per cent. Agral LN solution. The solution of DDT consisted of DDT in a solvent containing 78 parts by volume of xylene, 20 parts of ethylene glycol monoethyl ether and two parts of liquid paraffin. This mixture spreads on glass and dries to leave an even film of DDT/liquid paraffin. Concentrations of DDT up to 0.15 per cent. w/v can be dissolved in this solvent without the ultimate film crystallising.

Analysis of performance.

Results.

The method has so far been used mainly with house-flies, with insecticide deposited on glass plates or cabbage leaves. The behaviour of some other insects in the chamber is also described below.

It was found most convenient to keep the time of exposure constant in any particular experiment, and to obtain the different doses required for drawing a probit line by varying the deposit densities. This makes it easier to compare one experiment with another, as there are day-to-day variations in the levels of deposit given by the spraying tower which cannot be eliminated. The toxicity of glass plates sprayed with DDT emulsion increased over a period of days as the deposit progressively crystallised.

The performance of the apparatus was tested using plain glass plates, wax-coated plates or cabbage leaves as the test surface. On plain and wax-coated glass plates, emulsion gave deposits that crystallised irregularly, and gave very variable results. Emulsion deposits were more toxic on cabbage leaves, and the results were much more uniform. The liquid-paraffin formulations gave deposits of low toxicity on leaves, perhaps because the solvent soaked into the leaf;

* A non-ionic wetting agent supplied by Messrs. Plant Protection, Ltd.

consequently, this combination of formulation and test surface was not used. Suspensions were satisfactory on both leaves and plates.

Effect of repeated exposures.

When the same plate is used for several batches of insects, the toxicity of the deposit must fall as insecticide is removed by each batch. To test the extent of this effect, 20 batches, each of ten house-flies, were exposed successively on the same plate. The mortalities obtained are shown in fig. 3, each point representing

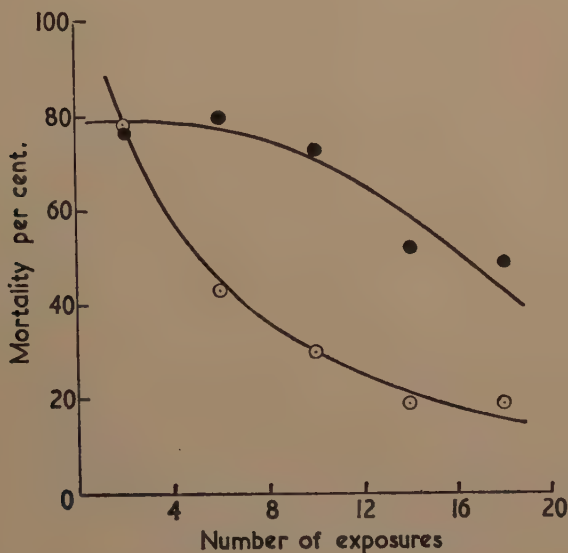


Fig. 3.—Mortality produced by a single glass plate bearing a deposit of DDT when successive batches of ten house-flies each were exposed to it. Each point represents the mean mortality of four batches of flies. ○, liquid deposit of DDT in liquid paraffin, $1.4 \mu\text{g./cm.}^2$ of DDT. ●, crystal-line deposit from a suspension, $2.2 \mu\text{g./cm.}^2$ of DDT.

the mean of four successive batches to reduce random scatter of the points. The deposits used were suspension on glass ($2.2 \mu\text{g./cm.}^2$ of DDT) and DDT/liquid paraffin ($1.4 \mu\text{g./cm.}^2$ of DDT). With suspension, there is little loss of toxicity until 12 groups of insects have been exposed, whereas the liquid-paraffin deposit loses toxicity in the first few exposures, perhaps because it is more effectively picked up by the insects. In the later work, except where specially mentioned, plates were used for not more than three batches of insects.

Replication of kill between batches.

When several groups of insects are given the same exposure on identical deposits, the variation in mortality from one group to another should result entirely from the random choice of insects when the groups are counted out, *i.e.*, the sampling error. The variance due to the sampling error can be calculated from statistical principles, and compared with that found experimentally.

Twenty-three groups of house-flies were exposed (4 min.) to plates sprayed with DDT suspension ($1.8 \mu\text{g./cm.}^2$) and the mortality was counted. On the next day, the experiment was repeated, using the same 23 plates (of which one

had to be discarded during the experiment), but a 5-min. exposure, as the mortality resulting from the 4-min. exposure was rather low. The mortalities of each experiment were then analysed statistically. For the first experiment, $\chi^2 = 46.1$ (21 degrees of freedom); this is significantly heterogeneous at $P = 0.01$. For the second experiment, $\chi^2 = 20.0$ (20 degrees of freedom); this is not significantly heterogeneous. Burt & Ward (1955) showed that deposits from DDT suspension increase in toxicity to *Tribolium castaneum* (Hbst.) when stored; it appears that during the first 24 hours there is also an increase in the replicability of the contact effect of the deposit. In later experiments with suspension deposits on glass plates, the plates were sprayed on the day before they were used.

Replication of kill on plates sprayed with DDT/liquid paraffin was tested by a slightly different experiment. Seven plates were used, and three successive batches of house-flies were exposed on each. For the twenty-one results, $\chi^2 = 32.0$ (20 degrees of freedom). This is just significantly heterogeneous at $P = 0.05$. When the three results for each plate were averaged to give a variance between plates, $\chi^2 = 5.9$ (6 degrees of freedom—not significant), so that the heterogeneity does not arise from variations in deposit level from one plate to another. The mean percentage mortality for the first, second and third exposures on all plates was 87, 78 and 76, respectively, showing the expected downward trend, but even when a correction was made for this by calculating the variance separately for each of the three exposures and combining the results, the χ^2 test still showed that the results were heterogeneous. This departure from the ideal result may be due to minor variations in behaviour between different groups of insects while on the test surface, which might result from slight differences in the degree of excitement of the flies when introduced into the chamber. In tests of insecticidal deposits, it is not possible to achieve identical treatment of the insects from one batch to another, so that the variance must be expected to exceed that due to the initial random choice of the insects, and this results in a heterogeneity factor greater than unity. The heterogeneity is small and seems not to cause heterogeneous probit lines when enough replicates are used.

Probit lines: replication between experiments.

Nine probit lines were determined, in separate experiments with house-flies, using deposits of DDT/liquid paraffin, with an exposure time of five minutes (Table I). The values for LD50 range from 0.69 to 1.45 $\mu\text{g./cm.}^2$ and the slopes

TABLE I.

LD50's, probit-line slopes and values of χ^2 obtained by exposing house-flies to deposits of DDT in liquid paraffin on glass plates. About 40 insects were used for each point. Only Exp. 62 gave a result that was significantly heterogeneous ($P = 0.05$).

Experiment	LD50 and S.E. ($\mu\text{g./cm.}^2$ DDT)	Slope and S.E.	χ^2	Degrees of freedom
58	0.80 \pm 0.06	3.0 \pm 0.6	3.0	3
59	0.69 \pm 0.05	4.6 \pm 1.0	2.2	3
60	0.76 \pm 0.03	6.2 \pm 0.7	3.2	3
61	0.82 \pm 0.05	4.1 \pm 0.7	4.4	2
62	1.30 \pm 0.28	2.8 \pm 1.0	16.3	4
63	0.89 \pm 0.06	5.0 \pm 0.8	1.9	4
64	1.45 \pm 0.10	5.3 \pm 0.8	9.5	4
65	1.15 \pm 0.07	6.2 \pm 0.8	0.7	2
66	0.80 \pm 0.04	5.8 \pm 0.6	4.4	4

of the lines range from 2.8 to 6.2. The lines are rather more steep than is usual in this type of test; steep lines are useful when it is necessary to discriminate between two formulations differing only a little from one another in toxicity, but they make the experimental procedure rather more difficult, as they magnify the effect on kill of random variations in the deposit density of the plates, and increase the chances that the range of concentrations used in an experiment will be either too high or too low. Of the nine experiments, only one (Exp. 62) gave a result that was significantly heterogeneous.

In seven successive experiments with house-flies, probit lines were determined for deposits from DDT emulsion on cabbage leaves. The leaves were sprayed 24 hours before use. In fig. 4, all the points except those giving zero or 100 per

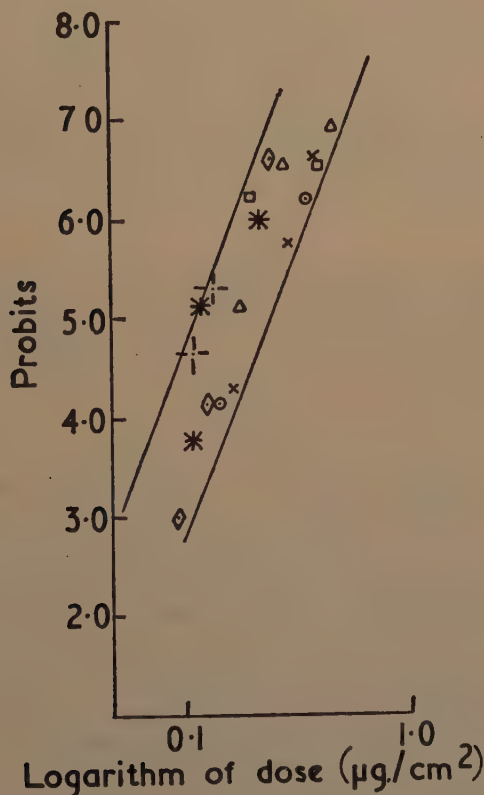


Fig. 4.—Points obtained from seven experiments in which house-flies were exposed to DDT emulsion on cabbage leaves. Each point represents the mortality from four batches of ten flies at the given concentration. One symbol indicates results from one experiment.

cent. mortality are plotted. The lines are all very steep, with a mean slope of about 8.0. Lines as steep as this give a close estimate of the LD50, but they generally provide too few useful points to permit a calculation of the best-fitting line or the confidence limits. The range of concentrations of spray used was chosen to give a ratio from one deposit to the next of about 2:1.

Nothing is gained by attempting to use a more closely spaced range, because of the random variations in deposit on plates sprayed in the Potter tower. But, although no statistical analysis can be given, all the points in fig. 4 can be enclosed between two parallel lines, which intersect the 50 per cent. mortality abscissa at deposit levels of 1.4 and 2.7 $\mu\text{g./cm.}^2$ This is no greater than the usual variation in resistance of test insects from one culture to another. The method, therefore, can give reproducible results.

Effect of variation in the conditions of test.

The effect of variations in the temperature of the hot-plate was studied in two experiments, using house-flies. Plates were sprayed with the DDT/liquid paraffin formulation, and probit lines were determined with the surface temperature of the hot-plate at 32°C. and at 47°C. The increase in temperature decreased the LD50 by 10 per cent. and 20 per cent., respectively, in the two experiments. Small variations in the hot-plate temperature will therefore have no significant effect on the results.

In Table II the results are given of two early experiments in which the toxicity to house-flies of a DDT/liquid paraffin deposit was tested, varying the period of exposure and keeping the deposit density constant. This shows the slope of lines obtained in this way.

TABLE II.

Results obtained by exposing groups of house-flies for varying times to plates bearing deposits of DDT/liquid paraffin of the same density (1.4 $\mu\text{g./cm.}^2$ DDT). Mortalities are corrected for control deaths.

Exposure (minutes)	1	2	3	4	5	6
Mortality %, Exp. 18	3	35	27	67	79	90
Mortality %, Exp. 19	13	54	78	100	100	100

Several other insect species were tested in the exposure chamber, to see whether they would remain on the treated surface. Adults of *Aedes aegypti* (L.) were often seen to rest on the cold ring. Larvae of *Pieris brassicae* (L.) were sluggish, but did not seem to be repelled by the cold. Adults of *Phaedon cochleariae* (F.) and larvae of *Plutella maculipennis* (Curt.) were too small for the apparatus, but they might be used successfully if it were modified. *Blattella germanica* (L.) and *Tenebrio molitor* L. adults were repelled by the cold metal; the latter species does not require the use of this apparatus, as it cannot climb smooth vertical surfaces. Though the method of test is primarily intended for house-flies, it could probably be adapted for use with other insect species.

Summary.

Methods that have been used to confine insects to the test surface during exposure to insecticidal deposits are briefly reviewed, and their limitations are discussed. Some unsuccessful preliminary experiments on alternative methods are mentioned.

A temperature-preference method of inducing house-flies, *Musca domestica* L., to remain on a treated surface is described, and the apparatus is illustrated. The treated surface forms the floor of a chamber; it is maintained at a higher temperature than the walls and lid. The flies are introduced by means of a plunger device.

The variance in mortality among groups of house-flies given the same exposure was determined in three experiments. In the first, plates sprayed with a crystalline suspension of DDT were used immediately after spraying, and the variance was high. In the second, the same set of plates was used 24 hours later, and the results were not significantly heterogeneous. In the third, plates carrying a deposit of DDT in liquid paraffin were used, and the results were just significantly heterogeneous ($P = 0.05$). The heterogeneity is thought to have come from variations in the degree of activity of the house-flies while on the test surface; it was too small to affect probit lines obtained with the apparatus.

Nine successive experiments, in which the LD50 for house-flies of DDT/liquid paraffin on glass plates was determined, gave a range of results from 0.65 to 1.45 $\mu\text{g.}/\text{cm.}^2$ of DDT and probit-line slopes in the range 2.8 to 6.2. One of the experiments gave significantly heterogeneous results.

In seven separate experiments to determine the toxicity to house-flies of DDT emulsion sprayed on cabbage leaves, the probit lines were too steep for calculation by the normal method, but all the points fell between parallel lines intersecting the 50 per cent. mortality abscissa at 1.4 and 2.7 $\mu\text{g.}/\text{cm.}^2$, a variation in resistance no greater than is usual between different cultures of test insects.

The behaviour of some other insect species in the test chamber was observed. The apparatus would probably be suitable for use with *Blattella germanica* (L.) but some species failed to respond to the temperature gradient and others were too small for the apparatus as described.

Acknowledgement.

We would like to acknowledge helpful conversations with Mr. R. A. Harrison of the Plant Diseases Division, D.S.I.R., Auckland, New Zealand, while he was working in the Department.

References.

- BURT, P. E. & WARD, J. (1955). The persistence and fate of DDT on foliage. I. The influence of plant wax on the toxicity and persistence of deposits of DDT crystals.—*Bull. ent. Res.* **46** pp. 39–56.
- BUSVINE, J. R. (1957). A critical review of the techniques for testing insecticides.—208 pp. London, Commonw. Inst. Ent.
- DERBENOVA-UKHOVA, V. D. (1952). Flies of epidemiological importance. [*In Russian.*] Moscow.
- GRATWICK, M. (1957). The uptake of DDT and other lipophilic particles by blowflies walking over deposits.—*Bull. ent. Res.* **48** pp. 733–740.
- HADAWAY, A. B. & BARLOW, F. (1951). Studies on aqueous suspensions of insecticides.—*Bull. ent. Res.* **41** pp. 603–622.
- McINTOSH, A. H. (1947). Relation between particle size and shape of insecticidal suspensions and their contact toxicity. I. DDT suspensions against *Tribolium castaneum* Hb.—*Ann. appl. Biol.* **34** pp. 586–610.
- POTTER, C. (1952). An improved laboratory apparatus for applying direct sprays and surface films, with data on the electrostatic charge on atomized spray fluids.—*Ann. appl. Biol.* **39** pp. 1–28.

THE GREEN SCALES OF COFFEE IN AFRICA SOUTH OF THE SAHARA
(HOMOPTERA, COCCIDAE).

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This paper—third of the series on the representatives of the genus *Coccus*—deals with the identity of *C. viridis* (Green), *africanus* (Newst.) and a small group of related species collected during a survey recently carried out in Kenya, Tanganyika and Uganda. Six different green scales, occurring on coffee in Africa south of the Sahara, are recognised here, and it is reasonable to assume that others remain to be found in the area under review.

The various species treated in the course of the present paper can be identified by the use of the following key:

- 1 (6) Dorsal setae spiniform.
- 2 (3) Ventral multilocular disc pores about genital opening only ... *africanus*.
- 3 (2) Multilocular disc pores extending in transverse rows on all abdominal segments.
- 4 (5) Tubular ducts present on the marginal and submarginal ventral areas as well as near the attachment of each leg and extending across the median area of the thorax *celatus*.
- 5 (4) Tubular ducts occurring on the marginal and submarginal ventral areas only *consimilis*.
- 6 (1) Dorsal setae cylindrical.
- 7 (10) Tubular ducts present near the attachment of the legs and extending across the median area of the thorax and first abdominal segment.
- 8 (9) Antennae with eight joints; tubular ducts numerous, some of which occur near the attachment of the front legs *alpinus*.
- 9 (8) Antennae with seven joints; tubular ducts rather few and never associated with the front legs *viridis*.
- 10 (7) Tubular ducts very few on either side of the genital opening only *viridulus*.

The holotype and seven paratypes of each species described as new in this paper have been deposited in the British Museum (Natural History), London; three paratypes in the U.S. National Collection of Coccidae, Washington, D.C.; and two paratypes in the Muséum National d'Histoire naturelle, Paris. The remainder are in the collection of the Scott Agricultural Laboratories, Nairobi, Kenya.

Coccus africanus (Newstead, 1898) (fig. 1).

1898. *Lecanium viride africanum* Newstead, Ent. mon. Mag. **34** p. 95, figs. 6-8.
 1906. *Lecanium viride africanum* Newstead—Newstead, Quart. J. Inst. comm. Res. Trop. Lpool **1** p. 71.
 1909. *Lecanium viride africanum* Newstead—Marchal, Mém. Soc. zool. Fr. **22** p. 181.
 1913. *Lecanium viride africanum* Newstead—Vayssière, Ann. Epiphyt. **1** p. 430.

In the first paper (De Lotto, 1957) dealing with the identity of some Ethiopian species of the soft-scale genus *Coccus*, a redescription of a green scale commonly known in East Africa as *C. africanus* (Newstead) was included. Although at that

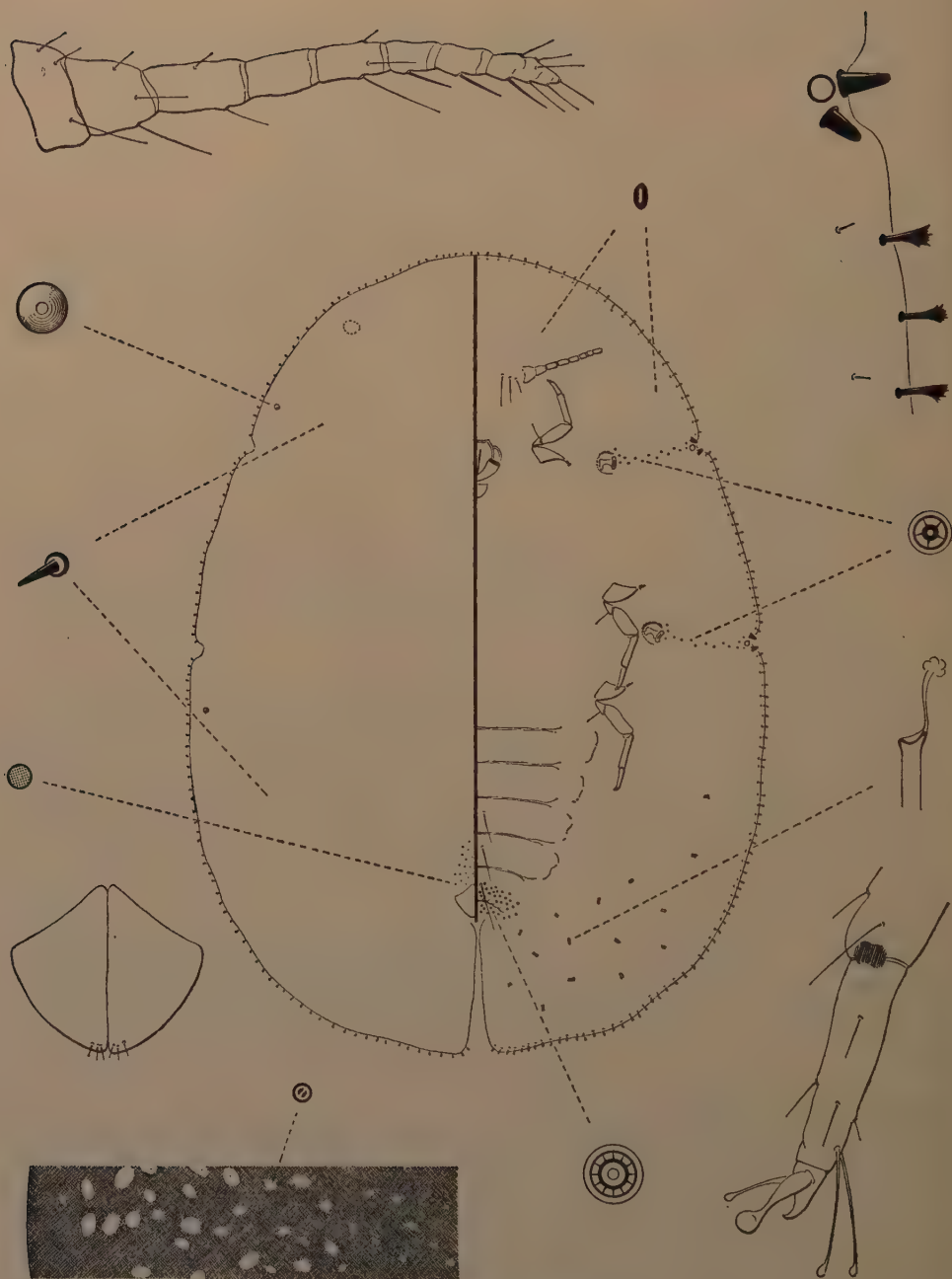


Fig. 1.—*Coccus africanus* (Newstead).

time the type had not been seen, the conclusions concerning its identity did not rest merely on the fact that the species had for many years been identified as such, but were in addition based on a detailed study of a long series of specimens which agreed reasonably well with a supplementary diagnosis of the species published by Newstead in 1917. This was correct in part only, because Newstead under the name of *africanus* confused two different species. It is pointless here to discuss details of Newstead's treatment of the matter. For the purpose of this paper, the situation—after having examined some of the types and other material studied by Newstead, and now located in the collections of the British Museum (Natural History)—can be summarised as follows. In 1898, Newstead first described *africanus* as a variety of *viridis* (Green) from specimens attacking coffee in Lagos, Nigeria. Later references, as listed above, were mere repetitions of the original record and did not contribute any new information towards the recognition of the species or its distribution. Newstead's next reference was in 1917, when he raised the variety to specific rank. It is unquestionable that, when viewed against all congeneric species known from Africa south of the Sahara, the form from Nigeria originally described by Newstead is well distinct, and his action was fully justified. Yet his conclusions on the differences between *viridis* and *africanus*, as well as the redescription of the latter, were made on specimens from coffee received from Uganda, which bear no relation to the original material from Nigeria. Thenceforth, the real *africanus* from Nigeria passed into oblivion and the name *africanus* has been used, for more than 40 years, to designate a different species occurring in East Africa.

The following redescription of *africanus* is made on a single original mounted specimen of the type series in poor condition.

According to the collector, Mr. C. Planch, quoted by Newstead (1898), "the insect is green in colour". No other details on its habit were given. Body broadly oval, 2.7 mm. long. Dorsal dermis moderately chitinated and marked by oval or rounded pale areas, which are fairly large and close together on the marginal and submarginal areas and tend to be progressively smaller and set widely apart towards the middle of the body. Each area encloses a minute circular pore. Dorsal setae very small, pointed and scattered. Tubercle-like pores small, flat, having a granular surface, arranged in a close group in front of the anal plates. Owing to the poor condition of the paratype specimen at hand, their exact number could not be determined. On one side of the body only, two submarginal tubercles could be seen; the actual number is probably larger. Anal plates together slightly wider than long, with three small apical setae; posterior-lateral margin broadly rounded; outer angle somewhat pointed. Setae of the marginal fringe short and robust, dilated and frayed at the apex, set rather close to one another. Stigmatic spines three; median spine of all stigmatic clefts broken away. Ventral dermis with a cluster of multilocular disc pores about the genital opening only. Quinquelocular pores in the stigmatic furrow few and arranged in an irregular row one pore wide. Tubular ducts very few and scattered on the marginal and submarginal areas of the last abdominal segments only. Small pores with an elongate opening widely distributed. The three abdominal segments anterior to the genital opening each provided with two robust setae. Legs all well developed with a prominent tibio-tarsal articulatory sclerosis; ungual digitules distinctly different in shape, one being very stout, the other slender; both are knobbed at the apex. Four setae apparently occur on the fold of the anal invagination. Antennae with eight joints.

NIGERIA: Lagos, August 1897, on coffee [*Coffea* sp.] (C. Planch).

This is the green scale to be known as *C. africanus*. Before the present revision was undertaken, Newstead's misunderstanding of the true identity of the species, and some misidentifications by later authors—the most important of

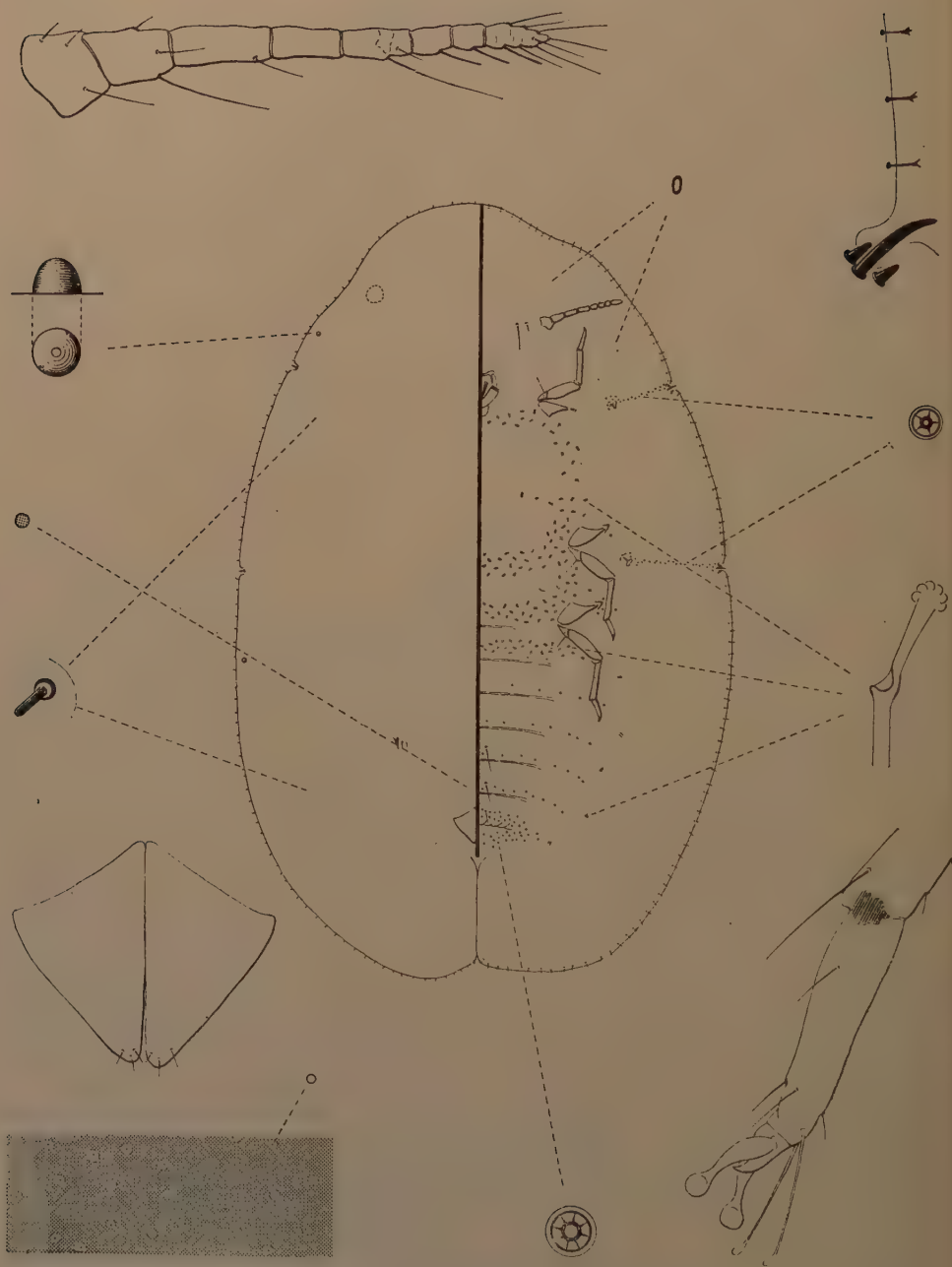


Fig. 2.—*Coccus alpinus*, sp. n.

which are dealt with below—resulted in *C. africanus* being regarded as widespread in Africa south of the Sahara. It seems likely that the species is instead confined to Nigeria. This view tends to be supported by the fact that none of the material of green scales from various other countries of western, eastern and southern Africa, examined for the purpose of this paper, revealed the presence of *africanus*.

***Coccus alpinus*, sp. n. (fig. 2).**

1917. *Lecanium africanum* Newstead—Newstead, Bull. ent. Res. 7 p. 357, fig. 11 [misidentification].
 1957. *Coccus africanus* (Newstead)—De Lotto, J. ent. Soc. S. Afr. 20 p. 296, fig. 1 [misidentification].

As mentioned above, the specimens on which Newstead raised *viridis* var. *africanus* to specific rank in 1917, and on which he based his redescription of the species, were different from those described originally from Lagos as *viridis* var. *africanus*; they were collected by C. C. Gowdey on coffee at Chagwe in Uganda. This species, which has since become well known in East Africa, requires to be renamed and is redescribed below as *C. alpinus*.

Living adults uniformly light green in colour, with a few greyish irregular small spots along the median area of the dorsum; moderately convex at maturity. Mounted specimens broadly to elongate oval, at times acutely pointed in front and somewhat asymmetric, owing to the position on the host plant; length up to 5 mm. Dorsal dermis in fully mature and well stained specimens, either plain and membranous or very slightly chitinated and marked by small circular or oval pale areas set widely apart, all attaining the same size, and each enclosing a minute circular pore. Dorsal setae small, cylindrical, widely scattered. Up to three or four small tubercle-like pores with a granular surface at times occur in front of the anal plates; they are hardly distinguishable from the minute pores of the dorsal pale areas. Submarginal tubercles normally one or two on either side of the body; occasionally as many as three or altogether missing on one side. Anal plates together somewhat wider than long with three or four small apical setae; posterior end and outer angle pointed. Setae of the marginal fringe very small, apically slightly frayed and set rather close to one another. Stigmatic spines three, of which the median is about three times as long as the laterals. Ventral dermis with rather numerous multilocular disc pores about the genital opening and extending in loose transverse rows on all preceding abdominal segments; three to five pores occur near the attachment of each hind leg, and occasionally one or two near each median one. Quinquelocular pores of the stigmatic furrow arranged in a row one pore wide. Tubular ducts fairly numerous near the attachment of each leg and extending across the median area of all thoracic and first abdominal segments; one or two ducts normally occur on the submedian area of each abdominal segment, laterad to each row of multilocular disc pores. Small pores with an elongate opening widely scattered. The three abdominal segments anterior to the genital opening each with two slender setae. Legs all well developed with a tibio-tarsal articulatory sclerosis; ungual digitules of the same size and shape. Fold of the anal invagination with three or four setae. Antennae with eight joints.

KENYA: Ruiru, 4.i.1959, twenty mounted adult females collected on either side of leaves and on branches of *Coffea arabica* L. (T. J. Crowe).—Coll. No. 2422.

Other records from eastern Africa are as follows. References to material from the same host in the same locality, even if collected at different dates, are omitted.

BELGIAN CONGO: Bukavu, 15.ii.1958 on *Coffea arabica* L. (D. J. McCrae).
 ERITREA: Asmara, 6.iii.1953 on *Carissa edulis* Vahl (*Andemeschiel Tuoldehai*).

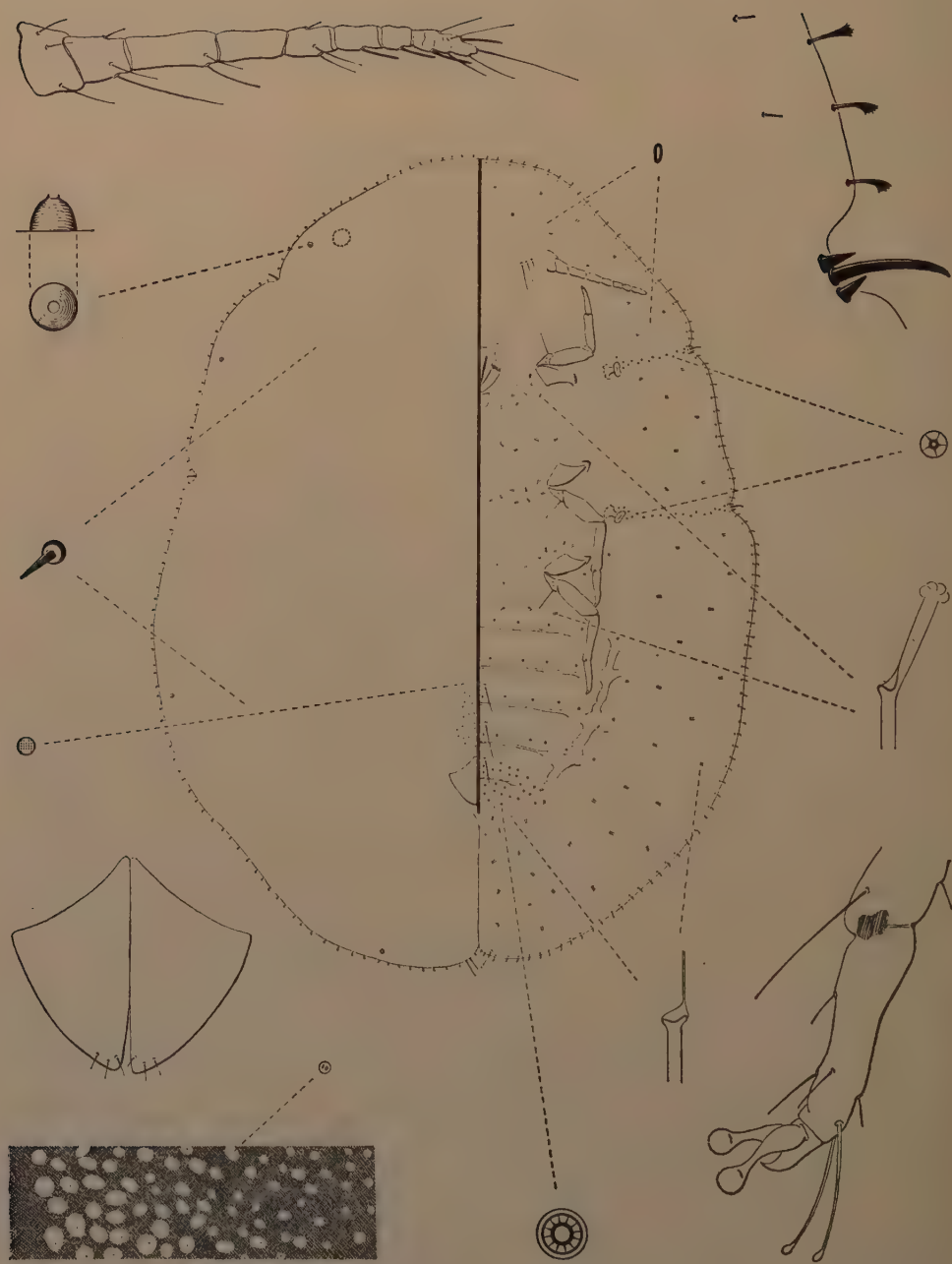


Fig. 3.—*Coccus celatus*, sp. n.

manot); Faghena', 27.v.1952 on *Citrus limonia* Osbeck (*V. Nastasi*). KENYA: Mitubiri, 4.xi.1937 on *Coffea arabica* L. (*R. H. Le Pelley*); Nairobi, 1.xii.1950 on *Gardenia* sp. (*M. S. Nattrass*), 9.i.1951 on *Coffea arabica* L. (*G. De Lotto*), 15.iii.1951 on *Coffea robusta* Lindl. (*do.*), 20.vi.1951 on *Ehretia silvatica* Guerke (*do.*), 24.viii.1951 on *Carissa edulis* Vahl, *Gymnosporia* sp. and *Psidium guajava* L. (*do.*); Teita Hills, 18.viii.1954 on *Coffea arabica* L. (*P. A. Jones*). TANGANYIKA: Lyamungu, 30.ix.1958 on *Coffea arabica* L. (*G. De Lotto*). UGANDA: Mwera, 13.iv.1913 on *Coffea* sp. (*C. C. Gowdey*); Chagwe, 12.xi.1912 on *Coffea* sp. (*do.*) [*ex* Newstead's collection No. 1933, labelled as *Lecanium* (*Coccus*) *africanum* Newstead, paratypes ♀ ♀].

Structurally *C. alpinus* is very closely allied to *viridis* (Green) from which it differs in having many more tubular ducts—some of which are always associated with the attachment of the front legs—and in having the antennae always with eight joints, instead of seven as is the case in *viridis*. According to field observations recently carried out in East Africa, the two species are also ecologically distinct; although they occur within the same area, they thrive at different altitudes. Thus, *viridis* is to be found in coastal and low-lying districts up to 3,000–4,000 ft., while *alpinus* occurs only in localities situated above that level.

***Coccus celatus*, sp. n. (fig. 3).**

1910. *Lecanium viride* Green—Newstead, Bull. ent. Res. 1 p. 187 [*misidentification*].

Living adults uniformly light-green in colour, moderately convex at maturity. Mounted specimens broadly oval, often asymmetric or distorted due to their position on the leaves of the host plant; length up to 3.5 mm. Dorsal dermis at maturity moderately chitinated and marked by oval or circular pale areas, each enclosing a minute pore. Along the marginal and submarginal areas of the body they are large and close to one another and tend to be smaller and widely separated towards the centre of the body. Dorsal setae rather small and pointed, few and scattered. Tubercle-like pores flat with a granular surface, set in a close group of about 80 in front of the anal plates. Submarginal tubercles three to six—occasionally seven—on either side of the body. Anal plates together slightly wider than long, with the outer angle acutely pointed; posterior-lateral margin evenly rounded; apex with three small setae. Setae of the marginal fringe short, dilated and frayed at the apex, often curved downwards, set fairly close to one another; viewed from the edge they appear pointed. Stigmatic spines three, of which the median is about three to four times as long as the laterals. Ventral side of the body with a small group of multilocular disc pores about the genital opening and extending in very loose transverse rows on all preceding abdominal segments; a few pores occur near the attachment of each hind leg. Quinquelocular pores of the stigmatic furrow rather few and arranged in a row one or two pores wide. Tubular ducts not numerous; a few occurring near the attachment of each leg and extending across the median area of the thorax and—occasionally—across the first abdominal segment. Other ducts are present all along the submarginal and submedian areas, progressively fewer and widely scattered anteriorly. Small pores with an elongate opening distributed without any particular pattern. Setae of the three segments anterior to the genital opening robust. Legs all well developed with a large tibio-tarsal articulatory sclerosis; ungual digitules of the same size and shape. Fold of the anal invagination with four setae. Antennae with eight joints, except in two specimens in which one of the antennae was eight-jointed, the other seven-jointed.

UGANDA: Kampala, 9.vi.1958, twenty mounted adult females collected on the underside of leaves of *Coffea robusta* Lindl. (*G. De Lotto*).—Coll. No. 2352.

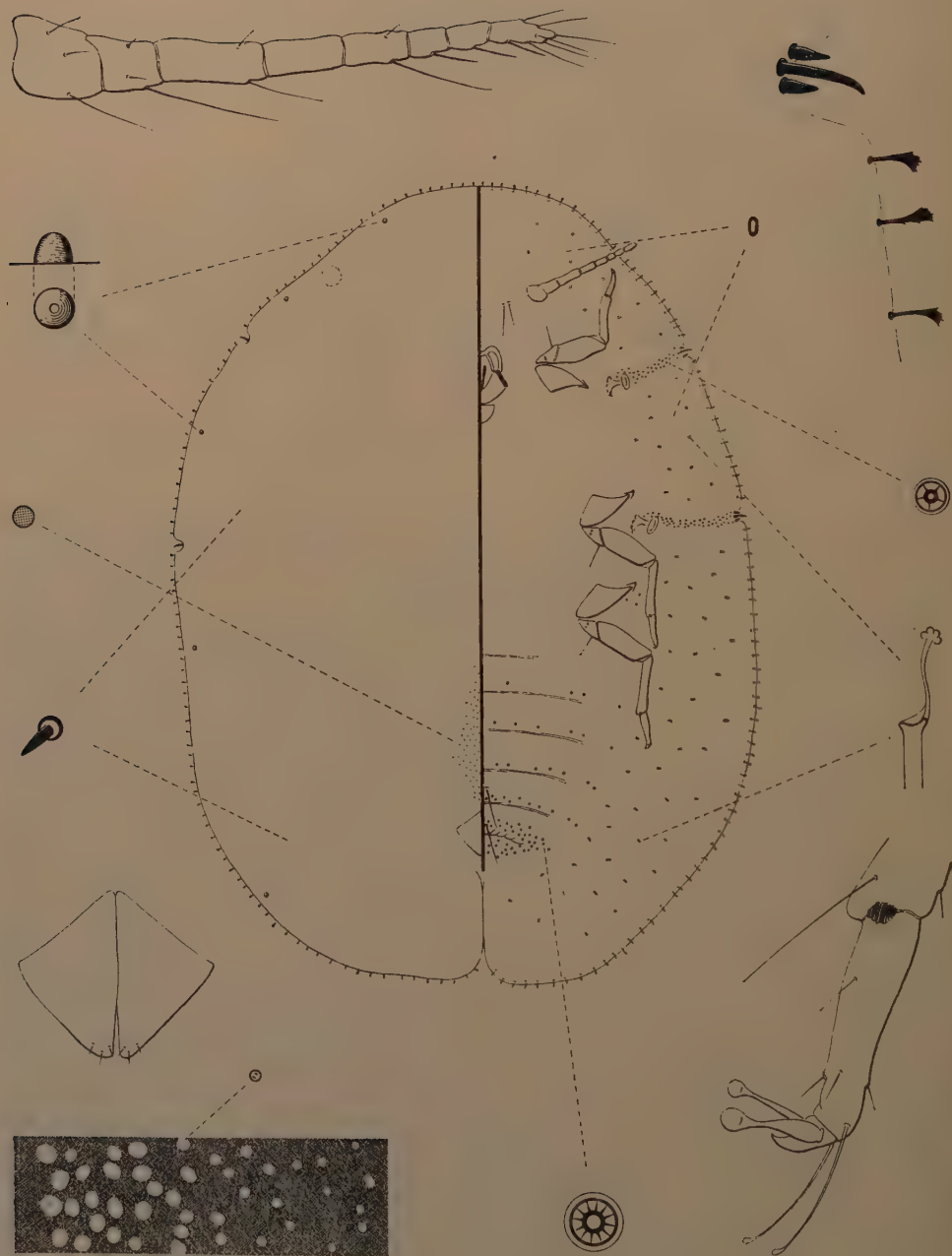


Fig. 4.—*Coccus consimilis*, sp. n.

All populations of this species were covered by a conspicuous shelter built by a biting ant, kindly identified by Mr. G. E. J. Nixon of the Commonwealth Institute of Entomology, London, as *Macromischoides aculeatum* Mayer.

The specimens, now in the collections of the British Museum (Natural History), which Newstead recorded in 1910 as *C. viridis* (Green) from Entebbe, Uganda, belong to this species.

***Coccus consimilis*, sp. n. (fig. 4).**

Living adults at maturity fairly strongly convex; colour bottle green with the marginal area lighter. Mounted specimens broadly oval, often somewhat asymmetric; length up to 4 mm. Dorsal dermis at maturity moderately chitinised and marked by oval or circular pale areas, which are fairly large and close together on the submarginal area of the body and tend to be progressively smaller and more widely separated towards the centre. Each pale area encloses a minute pore. Dorsal setae small, pointed, not numerous and scattered. Tubercle-like pores small, flat, with a granulate surface, and set in a group of about 100 in front of the anal plates. Submarginal tubercles normally four to six on either side of the body, at times reduced to two or as many as seven. Anal plates together slightly wider than long; outer angle pointed; posterior-lateral margin straight or slightly curved; apex with three small setae. Setae of the marginal fringe short and robust, dilated and frayed at the apex, set close to one another. Stigmatic spines three, of which the median is about twice as long as the laterals. Ventral dermis with moderately numerous multilocular disc pores about the genital opening, and a few extending in transverse loose groups on the four or five abdominal segments anterior to the genital opening. Quinquelocular pores fairly numerous and arranged in a band two or three pores wide. Tubular ducts few and scattered all along the submarginal and submedian areas; no ducts occur near the attachment of the legs or antennae. Small pores with an elongate opening scattered. Setae in front of the genital opening normally reduced to two couples only. Legs all well developed with a tibio-tarsal articulatory sclerosis; unguis digitules usually somewhat different in size, one being slightly smaller than the other; in a few specimens they attain the same size and shape. Fold of the anal invagination with four setae. Antennae with eight joints, except in four specimens in which one antenna was eight-jointed, the other seven-jointed.

UGANDA: Kampala, 7.vi.1958, twenty mounted adult females collected on *Coffea robusta* Lindl. (G. De Lotto).—Coll. No. 2353.

As a rule this species attacks the collar of the host plant, above or just below ground level.

***Coccus viridis* (Green, 1889) (fig. 5).**

- 1906. *Lecanium (Trechocoris) hesperidum africanum* Newstead, Quart. J. Inst. comm. Res. Trop., Lpool **1** p. 74 [*nomen nudum*].
- 1913. *Lecanium viride* Green—Lindinger, Jb. hamburg. wiss. Anst. **30** Beih. **3** p. 83.
- 1913. *Lecanium viride* Green—Vayssi re, Ann. Epiphyt. **1** p. 430.
- 1916. *Lecanium viride* Green—Green, Bull. ent. Res. **6** p. 375.
- 1918. *Lecanium viride* Green—de Seabra & Vayssi re, Bull. Soc. ent. Fr. **1913** p. 163.
- 1928. *Coccus viridis* (Green)—Laing, Entomologist **61** p. 215.
- 1957. *Coccus viridis* (Green)—De Lotto, J. ent. Soc. S. Afr. **20** p. 313.

Although some of the records of this species from Africa south of the Sahara have been found erroneous, its identity—as far as the types are concerned—does

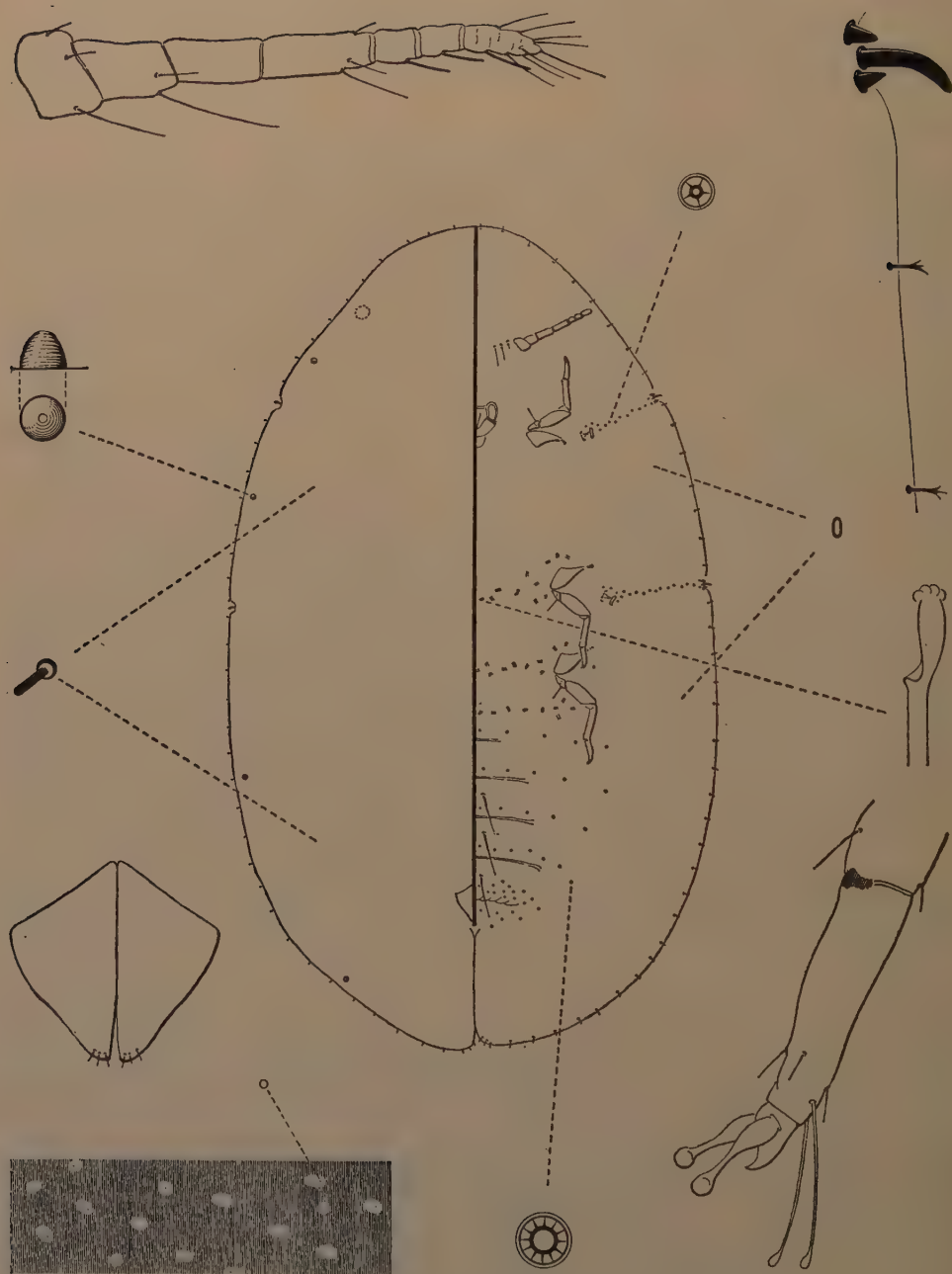


Fig. 5.—*Coccus viridis* (Green).

not present any particular problem. The following redescription is based on five paratypes *ex* Green's collection collected on coffee at Pundaluoya (Ceylon) and on a long series of specimens from East and West Africa.

"Adult female bright pale green, with an irregular, but very distinct loop of blackish spots on the middle of the dorsum (the contents of the malpighian tubules). . . . Dried examples become dull fulvous, and lose the chain of dark spots. Eyes conspicuous, black, close to margin. Anal scales minute, yellowish. Form oval; rounded behind, subacuminate in front; sometimes asymmetrical, the development on one side suppressed by contact with a prominent vein of the leaf. Moderately convex above, more particularly in females containing ripe ova. Margin very thin. Skin soft; never strongly chitinated. In old individuals the dorsum is almost smooth; but, before the body becomes tense with eggs, a slight median longitudinal, and two transverse ridges are noticeable, the latter above the stigmatic areas. Above the abdomen are three series of shallow depressions on each side of median ridge, defined by indistinct transverse and longitudinal ridges. . . . Length 2.5 to 3.25 mm. Breadth 1.5 to 2 mm." (Green, 1904.)

Dorsal dermis at maturity slightly chitinated and marked by small oval or rounded pale areas, all attaining more or less the same size; each pale area encloses a minute circular pore. Dorsal setae small, cylindrical, widely scattered. Tubercle-like pores usually missing, but at times one to four occur in front of the anal plates. They are small, flat and have a granular surface. Submarginal tubercles two to five on either side of the body. Anal plates together quadrate, with three or four small apical setae; posterior-lateral margin slightly rounded or inwardly curved distally; outer angle pointed. Setae of the marginal fringe very small and slender, slightly frayed at the apex, set rather widely apart from one another. Stigmatic spines three, of which the median is about two or three times as long as the laterals. Ventral dermis with rather few multilocular disc pores about the genital opening and extending in loose transverse rows in all the preceding abdominal segments; a few occasionally occur near the attachment of the hind legs. Quinquelocular pores of the stigmatic furrow arranged in a row one pore wide. Tubular ducts rather few and set near the attachment of the middle and hind legs and extending across the median area of the meso- and metathorax and the first abdominal segment. Very rarely one or two pores occur near the attachment of the fore legs. Small pores with an elongate opening widely scattered. Setae on the segments anterior to the genital opening set in three pairs; all slender. Legs well developed with a small tibio-tarsal articulatory sclerosis; ungual digitules of similar size and shape. Fold of the anal invagination with four setae. Antennae with seven joints.

The following material from Africa south of the Sahara has been examined: GHANA: Tafo, 20.xi.1945 on *Rauwolfia vomitoria* Afzel. (*E. O. Boaso*). KENYA: Kisumu, 6.vi.1958 on *Plumeria acutifolia* Ait. (*G. De Lotto*); Mombasa, 1.xi.1956 on *Citrus* sp. (*R. H. Le Pelley*), 18.ii.1959 on *Coffea robusta* Lindl. (*G. De Lotto*). NIGERIA: Ibadan, no date, on *Citrus* sp. (*V. Eastop*). PRINCE: S. Antonio, no date, on coconut [*Cocos* sp.] (*F. J. Simmonds*). SIERRA LEONE: November 1933 (*E. Hargreaves*). No other data recorded. TANGANYIKA: Lyamungu, 22.vii.1958 on *Coffea arabica* L. (*G. De Lotto*); Maramba, 4.x.1956 on coffee [*Coffea* sp.] (*P. T. Walker*). UGANDA: Kyadondo, 2.v.1957 on *Coffea robusta* Lindl. (*D. N. McNutt*). ZANZIBAR: 14.ii.1956 on *Coffea robusta* Lindl. (*R. H. Le Pelley*), 15.v.1958 on *Croton* sp. (*F. J. Graham*).

In East Africa, *C. viridis* occurs in coastal and low-lying areas and up to an altitude of 3,000 to 4,000 ft., and does not rank as a serious pest.

***Coccus viridulus*, sp. n. (fig. 6).**

Living adults shallow convex; colour uniformly light green, with a few blackish spots along the median area of the dorsum. Mounted specimens broadly oval or

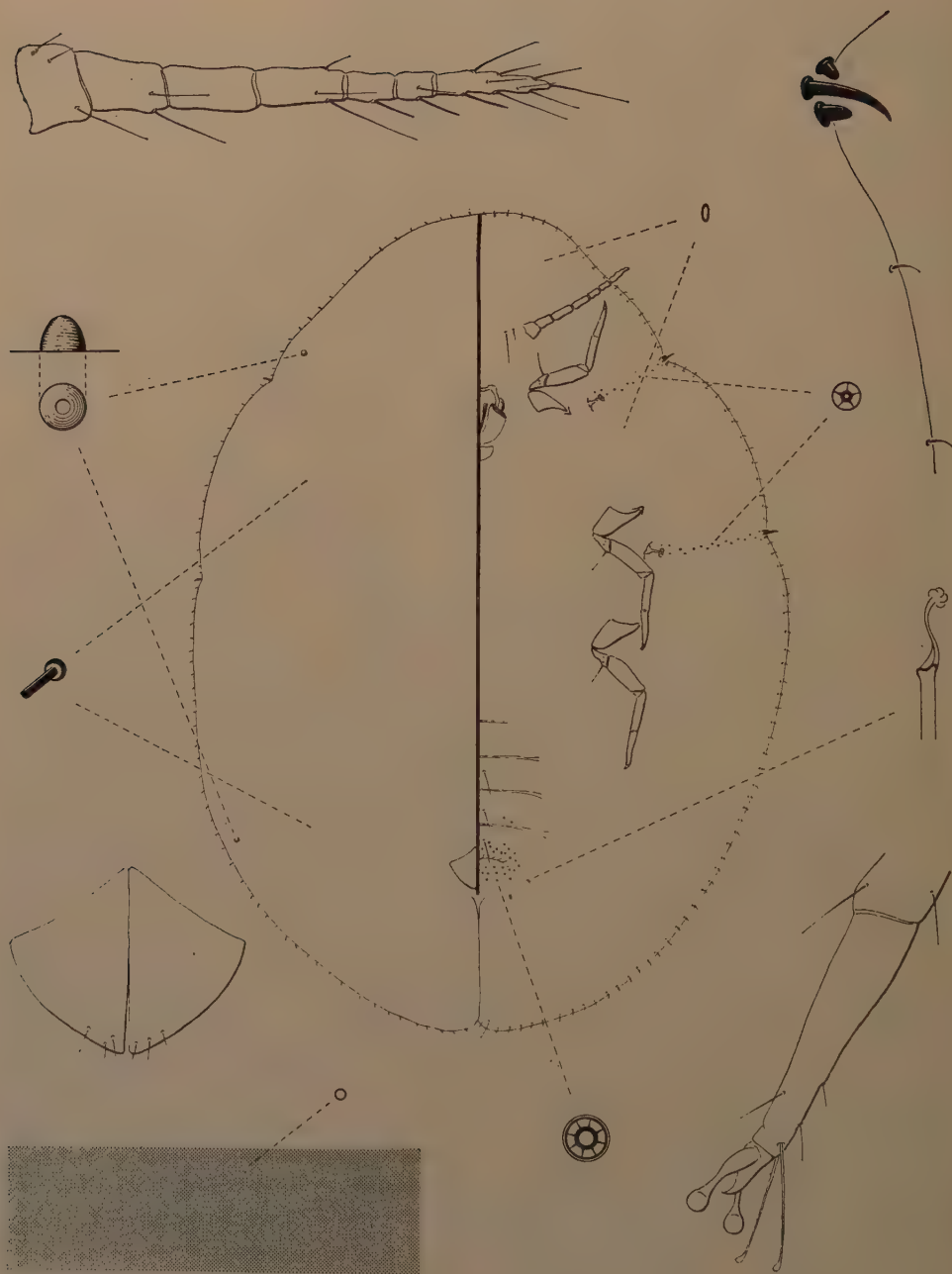


Fig. 6.—*Coccus viridulus*, sp. n.

elliptical, often asymmetric, up to 2.5 mm. long. Dorsal dermis at maturity very slightly chitinated and marked by very small circular pale areas set very widely apart from one another and having a minute pore in the centre; numerous other pale areas, larger, irregularly shaped and very poorly defined occur all along the marginal area of the body; they are set radially and are devoid of pores. Dorsal setae small, cylindrical, few and scattered. No tubercle-like pores anterior to the anal plates. Submarginal tubercles one to three on either side of the body. Anal plates together wider than long, with three or four small apical setae; posterior-lateral margin straight or broadly curved; outer angle pointed. Setae of the marginal fringe very small, mostly finely pointed and curved downwards; a few are slightly fimbriate at the apex; they are set widely apart from one another. Stigmatic spines three, of which the median is about two or three times as long as the laterals. Ventral dermis with few multilocular disc pores about the genital opening and the preceding segment; one or two pores at times occur on the penultimate and antepenultimate segments. No pores occur near the attachment of the hind or middle legs. Quinquelocular pores of the stigmatic furrow few and arranged in a row one pore wide. Tubular ducts not more than one to three on either side of the genital opening. Glands with an elongate opening few and scattered. Each of the three segments anterior to the genital opening with two slender setae. Legs all well developed; tibio-tarsal articulatory sclerosis absent; ungual digitules attaining the same size and shape, both stout and knobbed at the apex. Fold of the anal invagination with four setae. Antennae with seven joints, except for four specimens in which one of the antennae was reduced to six joints.

KENYA: Nandi Hills (6,100 ft.), 3.ii.1959, twenty mounted adult females collected on either side of leaves and on branches of *Coffea arabica* L. (G. De Lotto).—Coll. No. 2436.

Coccus aethiopicus De Lotto, 1959.

1917. *Lecanium* (*Coccus*) *viride* Green—Newstead (in part), Bull. ent. Res. **8** p. 130 [misidentification].
 1920. *Lecanium africanum* Newstead—Brain, Bull. ent. Res. **11** p. 4 [misidentification].
 1959. *Coccus aethiopicus* De Lotto, J. ent. Soc. S. Afr. **22** p. 156, fig. 2.

This species has been recently described as new from specimens attacking *Citrus* sp. in South Africa (De Lotto, 1959). In some of its dermal characteristics it comes closer to the *C. hesperidum* group than to any of the green scales reviewed in the preceding pages.

The specimens on which Newstead based his record of *viridis* from South Africa (Newstead, 1917b) and those which Brain, from the same country, recorded as *africanus*, were all found to be referable to *aethiopicus*. It is strongly suspected that neither *africanus* nor *viridis* actually occurs in South Africa.

Summary.

The true identity of the specimens from Africa recorded as *Coccus africanus* (Newst.) and *C. viridis* (Green) is reviewed in detail. Four other species of green scales attacking coffee in Africa south of the Sahara are described as new. These are: *C. alpinus*—for more than 40 years confused with *africanus*—*C. celatus*, *C. consimilis* and *C. viridulus*.

Acknowledgements.

The writer wishes to convey his thanks to Dr. D. J. Williams, Commonwealth Institute of Entomology, London, who made available type material of *Coccus viridis* and *C. africanus* and a large amount of other material of green scales from the collection of the British Museum (Natural History); and to Dr. H. K. Munro, Department of Agriculture, Pretoria, for the loan of slides from Brain's collection.

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References.

- BRAIN, C. K. (1920). Coccidae of South Africa. V.—*Bull. ent. Res.* **11** pp. 1–41.
- DE LOTTO, G. (1957). On some Ethiopian species of the genus *Coccus* (Homoptera: Coccoidea: Coccidae).—*J. ent. Soc. S. Afr.* **20** pp. 295–314.
- DE LOTTO, G. (1959). Further notes on Ethiopian species of the genus *Coccus* (Homoptera: Coccoidea: Coccidae).—*J. ent. Soc. S. Afr.* **22** pp. 150–173.
- DE SEABRA, A. F. & VAYSSIÈRE, P. (1918). Les coccides de l'île de San Thomé (Hem.).—*Bull. Soc. ent. Fr.* **1918** pp. 162–164.
- GREEN, E. E. (1904). The Coccidae of Ceylon. Part III.—pp. 171–249. London, Dulau.
- GREEN, E. E. (1916). Report on some Coccidae from Zanzibar, collected by Dr. W. M. Aders.—*Bull. ent. Res.* **6** pp. 375–376.
- LAING, F. (1928). A list of the Coccidae of San Thomé.—*Entomologist* **61** pp. 214–215.
- LINDINGER, L. (1913). Afrikanische Schildläuse. V. Die Schildläuse Deutsch-Ostafrikas.—*Jb. hamburg. wiss. Anst.* **30** Beih. 3 pp. 59–100.
- MARCHAL, P. (1909). Contribution à l'étude des coccides de l'Afrique occidentale.—*Mém. Soc. zool. Fr.* **22** pp. 165–182.
- NEWSTEAD, R. (1898). Observations on Coccidae. XVII.—*Ent. mon. Mag.* **34** pp. 92–99.
- NEWSTEAD, R. (1906a). Identifications of Egyptian insect pests: list of other known African species.—*Quart. J. Inst. comm. Res. Trop., Lpool* **1** pp. 68–72.
- NEWSTEAD, R. (1906b). Report on insects sent from the Kaiserliche Biologische Anstalt für Land- und Forstwirtschaft, Dahlem, Berlin.—*Quart. J. Inst. comm. Res. Trop., Lpool* **1** pp. 73–74.
- NEWSTEAD, R. (1910). Some further observations on the scale insects (Coccidae) of the Uganda Protectorate.—*Bull. ent. Res.* **1** pp. 185–199.

NEWSTEAD, R. (1917a). Observations on scale-insects (Coccidae). III.—*Bull. ent. Res.* 7 pp. 343–380.

NEWSTEAD, R. (1917b). Observations on scale-insects (Coccidae). V.—*Bull. ent. Res.* 8 pp. 125–134.

VAYSSIÈRE, P. (1913). Notes sur les coccides de l'Afrique occidentale.—*Ann. Épiphyt.* 1 pp. 424–432.

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LARVAL MOVEMENT AND INFESTATION IN THE WHEAT BULB FLY, *LEPTOHYLEMYIA COARCTATA* (FALL.).

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The wheat bulb fly, *Leptohylemyia coarctata* (Fall.), usually lays its eggs in cracks and spaces in the top few mm. of bare soil. Cultivation of the soil may bury the eggs much deeper. The newly hatched larva, which is less than 2 mm. long, may then be forced to burrow up through the soil for as much as 230 mm. (9 in.) before it reaches the bulb of the young seedling.

The soil type may affect the degree of infestation attained. Larvae are known to be able to move successfully through 18 in. of sandy soil (Gough, 1946), but we have no published data for their behaviour in the peaty soil of the Fenland, where the heaviest infestations in Great Britain occur. We know that the wheat plant produces an exudate which is attractive to larvae (Stokes, 1956; Long, 1958); this exudate may be differently affected by different types of soil.

The experiments described in this paper were made to study the effect of three soil types on the infestation of seedlings after inoculation of pots with newly hatched larvae. The effect of differences of pH in clay-loam soil was also studied and plot experiments comparing two densities of wheat plant were made on this type of soil. The progress of the infestation on these plots was followed, to find out what happened to the larvae when they had exhausted the first shoots and were forced to seek another at a time when their food requirement was rapidly increasing.

Technique.

Pot experiments.

Three different types of soil were selected, peaty loam from the Fenslands near Peterborough, sandy loam from Bedfordshire and local clay loam from Long Hoos VII, Rothamsted Farm. The soils, which were known to be free from eggs of wheat bulb fly, were passed through a half-inch screen before use. Ten pots, 11 in. deep and 11 in. in diameter, were filled with each of the soils. As the pots were filled, the soil was pressed down to prevent it from sinking later. Each pot was fitted with a central open-ended glass tube 10 in. long and $\frac{1}{4}$ in. diameter placed vertically with the lower end 9 in. below the surface of the soil.

The pots were stood in the open and in mid-December were each planted with 20 freshly germinated wheat grains. Each pot was inoculated through the central tube with 20 freshly hatched wheat bulb fly larvae on 18th February using a long pipette as previously described (Long, 1958). Pots were examined on 8th March when all the plants were removed to the laboratory for dissection. Plant and larval incidence were recorded together with individual larval weight. Soil pH was also measured.

An experiment with soil pH controlled was set up the following August using clay loam from Rothamsted Farm known to be acid and to be free from eggs. After passing through a screen the soil was divided into four lots, the pH determined and calculated amounts of calcium carbonate thoroughly mixed with three of the lots to adjust their pH to 6.0, 7.0 and 8.0, respectively. The fourth lot was left untreated at its original pH of 4.9. The soils were then left exposed

to the weather for their pH to settle and were thoroughly turned over and tested at monthly intervals when further small amounts of calcium carbonate were added to correct the pH. In December, ten pots were filled with each of the clay soils and 12 with peaty loam. All these pots were fitted with central tubes as in the previous experiment.

The pots were each planted with 30 wheat seedlings; this number is large enough to avoid larval competition for plants. Other treatments were similar to those in the previous experiment. The pots were inoculated, each with 20 larvae on 28th March, and examined on 17th April. Soil pH for each treatment was again measured when it was found that the treated soils were slightly acid of their adjusted values.

Plot experiment.

Twelve fallow plots, seven ft. square, in the old kitchen garden at Rothamsted Lodge were covered with tarpaulins to prevent egg-laying during the oviposition period of wheat bulb fly from June till October. After removal of the tarpaulins, the soil was cultivated and left exposed. In early November the soil was again cultivated and sown with winter wheat, variety Cappelle, six plots at a seed rate of $1\frac{1}{2}$ bushels/acre and six at 3 bushels/acre. The rows were spaced seven in. apart with 12 rows in each plot.

Each plot was inoculated centrally between the middle two rows with 100 freshly hatched larvae from laboratory culture on 16th February. To inoculate, a core of soil two in. in diameter and three in. deep was removed and the larvae in 5 ml. of water were distributed over the floor of the hole before replacing the top soil.

In the plan for examining the development of the infestation, each plot was divided through the central inoculation point into four equal square sub-plots; each row in these sub-plots was divided into three-inch units by means of a gauge, and examined 5, 7, 10 and 12 weeks after inoculation. One sub-plot was selected at random from each plot on each of the four occasions, thus affording a total of six sub-plots for each plant density. Each sub-plot was completely examined, unit by unit, the plants being removed to the laboratory for dissection, as in the pot experiments.

When the plots were inoculated, an additional 30 larvae were put without food in petri dishes lined with damp filter paper and divided into two sets. One

TABLE I.

Effect of soil type on infestation of winter wheat by wheat bulb fly.

	Peaty loam	Sandy loam	Clay loam
pH	7.6	5.9	7.2
Number of pots	10	10	10
Plants			
Total number	193	200	190
No. of shoots	195	200	193
No. of damaged shoots	4	56	39
Larvae			
No. introduced	200	200	200
Total recovered	4	55	37
Dead larvae	0	7	1
Mean live weight (mg.)..	0.591	0.879	0.995

set was kept in a cold greenhouse and the other in a greenhouse that was free from frost. The larvae were examined each day and the number surviving recorded.

Results.

Effect of soil type on infestation.

Table I shows that the larvae traversed nine in. of soil and that plant infestation was most successful in sandy loam, less so in clay loam and that it nearly failed in peaty loam. The mean larval weight in the peaty loam was also appreciably smaller than in the other soils. The larvae grew fastest in the clay loam, two of them reaching the second instar. This was possibly because the plants were slightly more robust in the clay loam, many of them showing signs of producing a second shoot. In this they resembled those in the peaty loam. The smaller plants in the sandy loam also may have caused the larvae to begin leaving their shoots to search for another at a slightly earlier stage.

Six of the seven larvae which died in the sandy loam died because on three occasions two larvae infested the same stem. This led to the death of both larvae.

TABLE II.

Effect of soil type and pH on wheat bulb fly infestation of winter wheat.
(For details see text.)

				Clay loam				Peaty loam
pH	4.9	5.6	6.7	7.8	6.1
Number of pots	10	10	10	10	12
<u>Plants</u>								
Total number	300	300	299	299	365
No. of shoots	621	627	621	633	565
Shoots/plant	2.1	2.1	2.1	2.1	1.6
No. of damaged shoots	15	57	56	44	12
<u>Larvae</u>								
No. introduced	200	200	200	200	224
Total recovered	14*	47	46	34	9*
Dead larvae	2	9	15	10	3
Mean live weight (mg.)				0.330	0.419	0.379	0.533	0.323

* Significantly different from the others ($P < 0.05$).

Effect of soil type and pH on infestation.

A similar low level of infestation was obtained when the experiment was repeated, contrasting peaty loam with clay loam in which the pH of the latter was controlled (Table II). Unfortunately the pH of the peaty loam was not the same as in the previous experiment but when the infestation in the soil is compared with that in the equivalent clay loams of pH 6.7 and 7.8 it can be seen that the results in the peaty loams were probably not due to pH. The plants in the peaty loams had not made quite such good growth and this may have been responsible for the lower mean weight of the larvae.

The results also suggest that pH 4.9 may be too acid for the larvae. The plants developed quite normally at this pH but far fewer larvae infested them and the larval weight was low. Infestation was most successful between pH 5.6 and 6.7 and it is interesting to note that the sap pH of 6.2 obtained for wheat shoots falls midway in this range, which suggests a possible optimum at pH 6.2.

Effect of seed rate on spread of infestation in inoculated plots.

The larval infestation spread to similar extents in both low- and high-density wheat plots. In each plot the 84 ft. of row of wheat were divided into 336 units, each 3 in. long; 77 of these units enclosed the total area of infestation in both high and low densities (Table III). There were more plants near the release point

TABLE III.

The effect of seed rate on subsequent infestation in plants of winter wheat inoculated with newly hatched larvae. (Plots examined, 5, 7, 10 and 12 weeks after inoculation.)

Plant observations

Seed rate bushels/ acre	No. of units in infested area	Plants/ foot row	Total plants	Damaged plants	Percent- age plants damaged	No. of shoots damaged	Mean no. shoots damaged/ plant
1½	77	4.4	83	57	69	82	1.4
3	77	7.6	144	85	59	120	1.4

Larval observations

Seed rate bushels/ acre	No. released	No. recovered	Mean weight (mg.)		Distance (cm.) from release point	
			Week 5	Week 7	Mean	Maximum
1½	600	33	0.087	0.459	21.8	53
3	600	59	0.094	0.495	21.1	84

in the high-density plots and therefore more plants were subsequently damaged and more larvae recovered; nevertheless, in these plots the percentage of plants damaged was lower. Prolonged frost occurred for a few days in the period immediately after inoculation and may have impeded the establishment of the initial infestation. The larvae behaved in a similar way in both plant densities in damaging, on average, the same number of shoots in each plant attacked.

The effect of seed rate on level of infestation.

The number of larvae recovered was roughly in proportion to the two different plant densities, principally because plants being in the single-shoot stage at the time of infestation would normally bear only one larva each. Thus, the number of plants in the lower seed rate was 58 per cent. of the number in the higher seed rate and the number of larvae recovered was 56 per cent. of the number in the higher seed rate.

Effects of seed rate on larval size.

Plant density had little if any effect on the size of those larvae which find a host-plant; those in the high-density plots were a little heavier, which suggests they were growing slightly faster. By week 10, most of the larvae had pupated so that no further weight comparisons could be made.

Larval movements.

The maximum distance that a larva was found from the release point was 84 cm. (33 in.), and had the larva moved in a straight line this would represent the minimum distance it had travelled. However, larvae are thought to move in a more or less random manner, and therefore it is probable that the actual distance was much greater.

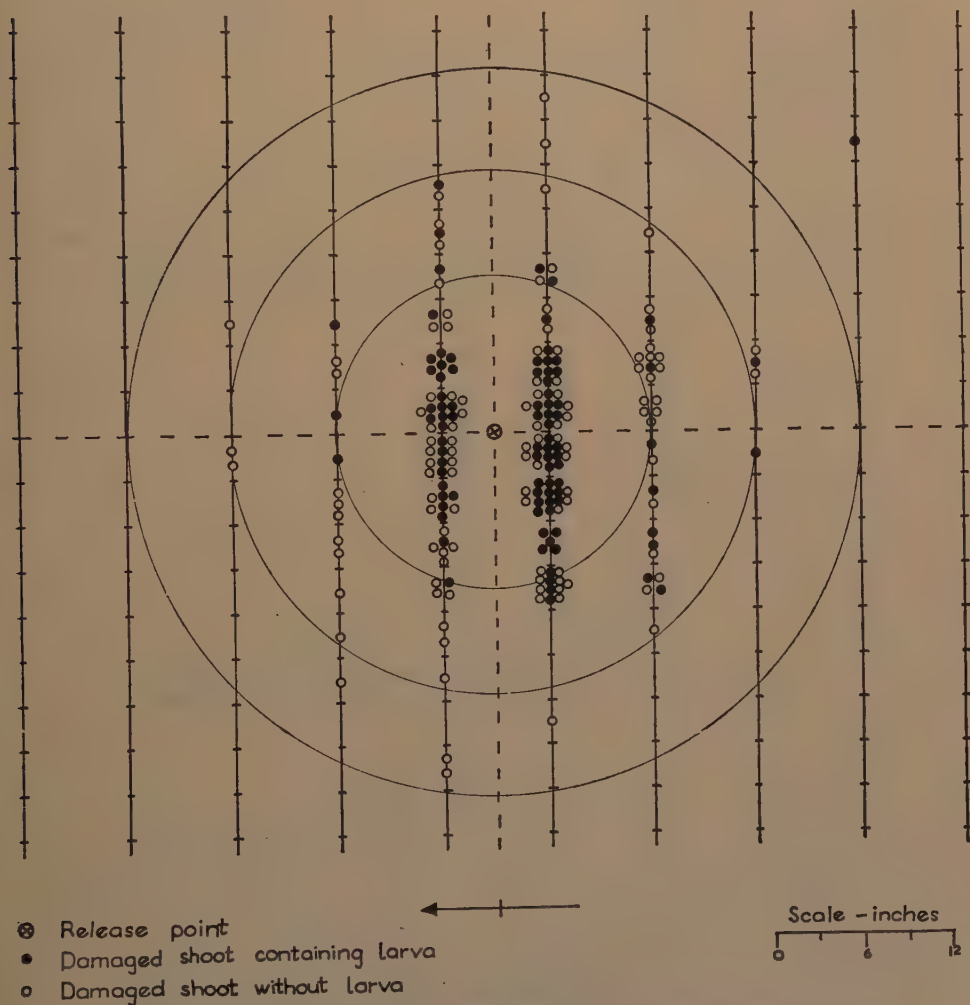


Fig. 1.—The spread of infestation after release of 1,200 newly hatched larvae of *L. coarctata*. (Total of all plots. For details see text.)

The larval distribution obtained from the total of all samples (fig. 1) shows that there was no predominating direction of larval movement, and fig. 2 shows that intensity of infestation was greatest near to the point of release.

The observations on the larvae in the greenhouse showed that larvae do not live long outside the host-plant. One half of those subjected to frost died between the fourth and fifth days, all being dead by the sixth day, whereas of those kept

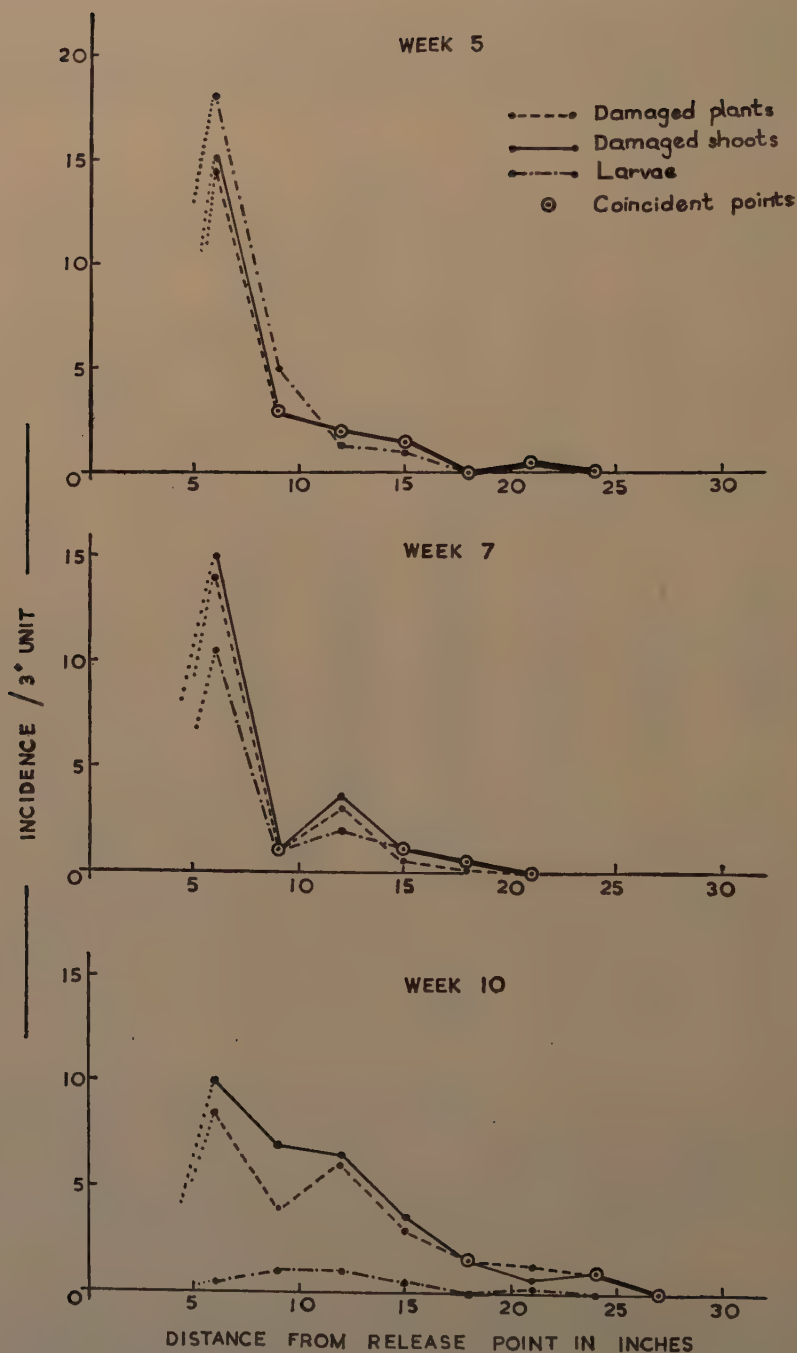


Fig. 2.—The movement of larvae of *L. coarctata* away from the release point with time, in relation to plant and shoot damage.

free from frost one half died between the eighth and ninth days and all were dead on the tenth day. Frost was prevalent for much of the immediate period after inoculation of the plots, so it seems probable that the initial infestation was established within a week of inoculation.

Because of early damage, some shoots had shrivelled or even disappeared by the tenth week and there was a small loss of data. By the twelfth week this loss was most evident and the precise number of shoots attacked could not, therefore, be determined. Accordingly, much of the subsequent study was restricted to data based on the first three sets of samples.

Plant counts showed that a mean of 5.0 plants/foot was maintained throughout the experiment and that there were no plants (as compared with shoots) killed by wheat bulb fly. When the first set of units was examined five weeks after inoculation, there was a mean of 1.1 larvae/damaged shoot. Very few larvae had moved out of their original shoots (figs. 2 & 3), so the larval distribution at that time represented the initial extent of the infestation, reaching a maximum of 38 cm. (15 in.) from the release point, although one damaged shoot was found at a distance of 21 in. (fig. 2).

Once a shoot is entered, a larva remains there for a time while feeding on the central growing portions; after this the larva leaves the shoot for another.

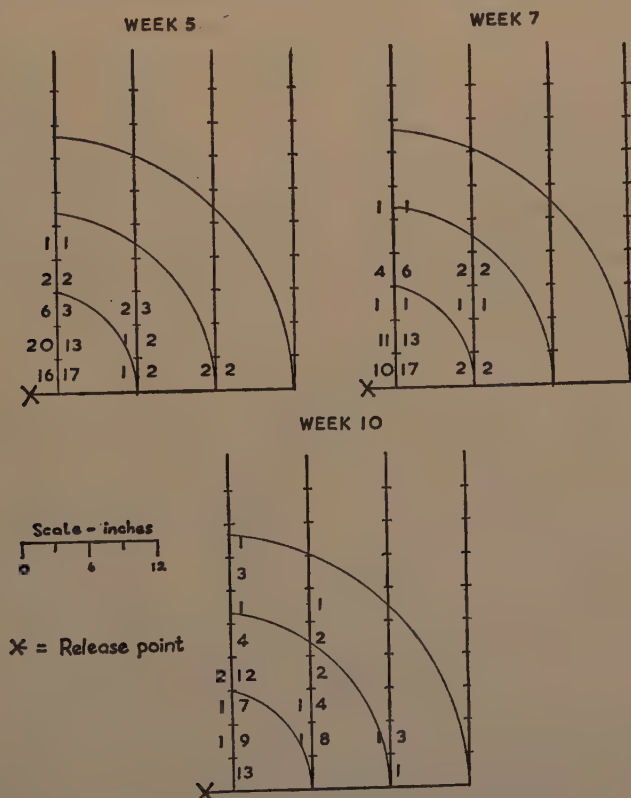


Fig. 3.—The movement of larvae of *L. coarctata* with time along and across rows in the sub-plots. (In each 3-in. unit left-hand figures = the total numbers of larvae; right-hand figures = total number of damaged shoots.)

This movement started seven weeks after inoculation, when empty damaged shoots were found in plants nearest to the release point; most of the movement occurred during the period of rapid larval growth before pupation (7th-10th week). Numerous empty damaged shoots were found and plant damage extended up to 61 cm. (24 in.) from the release point (fig. 2).

During the first seven weeks, while the infestation was static, the plants produced relatively few extra shoots, the mean number increasing from 1.1 to 2.0 shoots/plant. When older larvae were entering new shoots, the mean number had increased by the tenth week to 3.6 shoots/plant. Near the release point, where there were few unattacked plants, some of the larvae merely moved into a new shoot on the same plant: further away a shoot on an unattacked plant was generally selected. The tendency for movement to take place along the rows rather than across them is shown in fig. 3.

Larval survival and subsequent damage.

In the field, eggs hatch over a period of eight or more weeks and consequently larvae arrive only occasionally at the same shoot within a short time of each other. Other observations have shown that larvae which arrive later tend to select an uninfested shoot. Thus, only rarely will two or more larvae infest the same shoot.

In the experiment, however, many larvae reached the nearest plants to the release point within a very short time of each other, for several shoots in these plants contained two or more larvae. Thus, in the nearest rows to the release points (row I), 45 larvae were found in 36 shoots, nine of which contained two larvae and three had three larvae (week 5). When this occurred, they appeared to have a toxic effect on each other and frequently one or more of the larvae was found dead, although no sign of physical injury was detected. Never more than one of such larvae was found to be still alive at week 5, so this factor caused an appreciable mortality. Thus, 16 larvae died in this manner and left 29 still living before later movement of older larvae began. In adjacent rows (II & III) there were no stems containing more than one larva and there were no dead larvae.

TABLE IV.

The number of living larvae in the initial infestation and the total number of shoots damaged. (For details see text.)

Row		No. of live larvae at week 5	No. of damaged shoots at week 10	Ratio of damaged shoots/larva
I	29	50	1.7
II	4	17	4.3
III	2	4	2.0
Total	35	71	2.0

The data in Table IV suggest that very few larvae moved across the rows. Thus, the higher proportion of shoots/larva for row II and the lower value for row I suggests that only a few larvae (about four) had moved across from row I into row II. When the experiment ended at the twelfth week, one fully grown larva was found in row IV at a distance of 84 cm. (33 in.) from the release point, again showing that some larvae will cross rows in the later phase of movement. No relation was found between the distance travelled and the larval

weight. The proportion of the total number of damaged shoots at week 10 to the number of larvae surviving at week five was 71:35, that is, 2 shoots/larva.

Discussion.

In the experiments, many larvae presumably died in the establishment of the initial infestation. Thus, for sandy loam, which had the most successful infestation in the pot experiments, 72 per cent. of the larvae used for the inoculation were not recovered. This result is similar to Gough's (1946), whose data show 79 per cent. loss when eggs were buried eight or more in. in sandy soil. The clay loam of the pot experiment showed an 81 per cent. loss. In the plot experiment on clay loam, only 51 larvae out of a possible 300 (fig. 3) were recovered, *i.e.*, 83 per cent. were not accounted for at the first examination; this may have been partly due to the high larval density at the inoculation point, the affects of prolonged frosts and to the plants being in the single-shoot stage.

Much of the wheat in the United Kingdom infested with wheat bulb fly is grown in peaty soil and infestations of up to 80 per cent. of plants are frequent. In the pot experiments, however, larval losses of 96 to 98 per cent. occurred with peaty soil and infestation was limited to 2 per cent. of plants. The difference was probably due to the smaller depth larvae have to negotiate in the field compared with the pots, for Petherbridge, Stapley & Wood (1945) found that, even after ploughing, the majority of eggs were in the top three in. of soil. A deep ploughing experiment (10 in.) in peaty soil was followed by a reduced attack and was on one occasion accompanied by a large reduction in the number of eggs in the top 3 in.

In the pots, the larvae were inoculated at 9 in. and only just over 2 per cent. of plants in the peaty loam were infested. It may be inferred that this was associated with the nature of the soil and the depth of inoculation, for the pH was similar (7.6-6.1) to that of wheat sap (6.2) and the roots in both sandy and peaty soils reached the bottom of the pots. Whether the failure to infest in peaty soil is to be definitely attributed to either the physical characteristics of the soil or the influence of the soil state (or nutrition) on the production and fate of plant exudate needs further investigation. Successful infestations in the field show that peaty soil does not interfere excessively with the mechanism of host-plant location. Thus, the results suggest that the soil impeded larval movements to reach the surface layer (where the detection of the plant most frequently occurs (Long, 1958)) and finally the plant itself.

The plot experiment showed that freshly hatched larvae could travel at least 21 in. (53 cm.) in the initial phase of movement and probably at least a further 12 in. (30 cm.) in the later phase, when the larvae are much larger and may be expected to cover much greater distances: Gough (1946) found that third-instar larvae could traverse up to 18 in. Very little migration from the plant first infested had taken place by week 7 but by week 10 movement had been extensive and nearly four-fifths of the larvae had presumably pupated. Thus, about three-quarters of their larval life may be spent in the first shoot infested while their weight increases by a factor of 60: newly hatched larvae weigh about 0.0075 mg. and the mean weight at week 7 was 0.482 mg. (based on a recovery for that week of 8 larvae at the lower seed rate and 15 at the higher). Fully grown larvae attained a mean weight of 7.5 mg. in the experiments so that the weight increased by a further factor of about 15 during the last quarter of their life, while the larvae fed in another (and perhaps more than one more) shoot.

In the plot experiment, plants were spaced between $1\frac{1}{2}$ and 3 in. apart in the rows and the rows were 7 in. apart. Newly hatched larvae crossed rows in the initial infestation: but the older larvae tended to go more along rows, as is shown by the fact that at 10 weeks the infestation had not spread beyond the original

three rows, although it had spread along them (fig. 3). This suggests that the older larvae do not move at random to the extent shown by the younger ones but can detect an adjacent plant.

Summary.

In pot experiments, the ability of newly hatched larvae of the wheat bulb fly, *Leptohylemyia coarctata* (Fall.), to move through nine in. of soil and infest wheat plants was tested for three different types of soil: sandy loam, clay loam and peaty loam and also clay loams at different levels of acidity. Each soil was inoculated with 200 freshly hatched larvae and the effects associated with soil were measured by the number of larvae subsequently recovered from infested plants.

The larval recoveries for different soil types were: sandy loam 28 per cent., clay loam 19 per cent. and peaty loam 2 per cent. The larvae could infest plants grown in clay loam within a pH range of 4.9 to 7.8 and the results suggested a possible optimum at pH 6.2. The relative failure to infest in peaty loam appeared to be due to this soil impeding larval movement rather than interfering with the mechanism of host-plant location.

In plot experiments, no predominating direction of larval movement was observed. Newly hatched larvae can travel up to at least 21 in. (53 cm.) before they enter a shoot and feed. Three-quarters of the larval life may be spent in this shoot while the weight increases about 60 times. Additional distances are travelled when larvae leave this shoot to find another. This later movement tends to take place along rows. In subsequent feeding, larval weight increases by a further factor of 15. The larvae damaged an average of two shoots each and travelled up to a maximum distance of 33 in. (84 cm.), measured in a straight line, throughout their entire life-span.

Acknowledgements.

I wish to express my appreciation to Mr. R. G. Warren for repeated determinations of soil pH and advice on soil treatment and to Mrs. B. Copleston and Miss J. Balshaw for their assistance throughout the experiments.

References.

- GOUGH, H. C. (1946). Studies on wheat bulb fly (*Leptohylemyia coarctata*, Fall.). I. Biology.—*Bull. ent. Res.* **37** pp. 251–271.
- LONG, D. B. (1958). Host plant location by larvae of the wheat bulb fly (*Leptohylemyia coarctata* Fallén).—*Proc. R. ent. Soc. Lond.* (A) **33** pp. 1–8.
- PETHERBRIDGE, F. R., STAPLEY, J. H. & WOOD, J. (1945). Wheat bulb fly field experiments.—*Agriculture, Lond.* **52** pp. 351–354.
- STOKES, B. M. (1956). A chemotactic response in wheat bulb fly larvae.—*Nature, Lond.* **178** p. 801.

OCCURRENCE OF THE RED SPIDER, *OLIGONYCHUS COFFEAE*
(NIETNER), ON TEA IN NORTH-EAST INDIA IN RELATION TO
PRUNING AND DEFOLIATION. E.M.N

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The tea bush, *Camellia sinensis*, forms a thick canopy of leaves during the flushing season, and it is difficult to cover all the leaves with chemicals applied as sprays or dusts for effective control of pests. Furthermore, the choice of pesticides for use on tea, particularly during the plucking season, when most of the damage is caused by pests, is limited, as the questions of tainting the 'made tea' and of endangering consumers are involved (Das, 1959a). While the use of persistent chemicals is favoured from the point of view of efficiency in pest control, most of them cannot be used on tea during the plucking season unless leaves are discarded for one or two plucking rounds following treatment.

The red spider, *Oligonychus coffeae* (Niet.), is one of the major pests of tea in north-east India and difficulties encountered in dealing with this mite are greater than in the case of any other pest. More than two rounds of spraying are often required to control it during the plucking season, involving much loss of crop as a result of rejection of treated leaves when persistent chemicals or those tainting the made tea are used. Certain cultural practices, however, have a direct influence on its attack, and these will be discussed in this paper and elsewhere. The present paper deals mainly with the effects of pruning and defoliation on the mite incidence.

Persistence of red spider on tea bushes during the cold weather.

It was held that the red spider hibernates during the cold weather in the crevices of the bark of tea bushes and in the soil underneath them. This view was not accepted in a recent paper (Das, 1959b) where it was stated that the mite persists in all stages of its development on some of the old leaves of tea bushes during the cold weather, only in small numbers on clean pruned tea, but in greater numbers on unpruned or 'skiffed'* tea. It is this population that is primarily responsible for the build-up of the mite in the spring.

Counts of red spiders persisting on tea bushes during the cold weather were made (1) after plucking was over but before pruning, (2) after pruning but before cleaning out and (3) immediately after cleaning out†, in two adjacent plots, one planted with the Assam variety and the other with the China variety of tea. Twenty-five bushes were examined in five groups of five each from each plot (Table I).

It is evident from the table that some red spiders are harboured during the cold weather not only by old leaves (as has already been recorded by Andrews (1928) and Comrie (1939)) but also by 'janams‡'.

Clean pruning, however, removes a great portion of the mite population persisting on the bushes in the early part of the winter, but in unpruned or skiffed tea the reduction of the mite population is slight or negligible. Even after clean

* Shoots cut off just a little at the tops. In practice, tea is either pruned or skiffed. The term 'skiffed' is synonymous with 'unpruned' for the purpose of the article.

† Removal of dead snags, weak and crossing branches and banjhi (dormant) growth.

‡ Small leaves (cataphylls) at the base of the shoot.

pruning the China variety of tea, which is left with more leaves and janams, and consequently with more mites, than the Assam variety, suffers more from red-spider attack.

In districts where tea is subject to severe red-spider attack every year, pruned bushes are often defoliated by hand as a protective measure against future mite attack. Such areas of defoliated trees remain almost free from infestation in the spring, unless the attack spreads from the adjoining undefoliated areas. Complete defoliation removes those mites which persist on bushes after pruning. Most perish in the prunings and leaf-litter and the very few that may climb up the bushes can scarcely re-establish themselves if defoliation has been carried out before bud-break. Defoliation, therefore, appears to be a real safeguard against red-spider attack.

TABLE I.

Persistence of red spider on leaves of tea bushes during cold weather.

Kind and dates of treatment	Dates of observation	Variety of tea	Average number of		
			leaves (including 'janams') per bush	infested leaves (including 'janams') per bush	mites (including eggs) per bush
(1) Before pruning Last plucking 17.xi.58	1-3.xii.58	Assam	477.1	56.1	779.2
	4-6.xii.58	China	501.6	79.9	1778.5
(2) After pruning but before cleaning out Pruning 13-16.xii.58	23-26.xii.58	Assam	134.2	22.7	296.4
	26-27.xii.58	China	275.0	48.0	634.1
(3) After cleaning out Cleaning out 20.i.59	21-24.i.59	Assam	29.6	7.2	167.7
		China	45.9	6.8	255.0

In all experiments carried out in the past for control of red spider, the December spraying showed little benefit, and the treated plots were found to be as badly attacked as the untreated ones. Cold-weather spraying was not, therefore, advocated as a measure against red-spider attack (Harrison, 1937). Yet if the small population of the mite that persists on tea bushes during the cold weather is primarily responsible for subsequent attacks, there would appear to be no reason why cold weather spraying, if done efficiently, should not be as great a safeguard as defoliation. Furthermore, spraying should be more efficient immediately after pruning when there is less foliage than on flushing bushes at a later date.

Experiments and assessment of attack.

The intensity of red-spider attack was assessed in experiments carried out at Borbhetta Field Station on the effects of cultural treatments on crop of the Assam variety of tea. Observations of attack were also made on commercial estates, where uniform areas were selected from a section after treatment had been applied.

It is to be noted that the incidence of red spider, depending on various factors, varies from district to district, estate to estate and even from section to section

in the same estate. The results obtained for a particular treatment are, therefore, comparable with those of other treatments of the same experiment, but not with similar treatments of other experiments.

It may also be mentioned here that the red spider prefers mature leaves, and young leaves are not normally attacked, but in severe outbreaks when the growth of the bushes is checked, particularly under conditions of drought, both young and mature leaves may be equally attacked (Harrison, 1937; Das, 1959b).

The degree of infestation was assessed on all bushes in each plot by eye estimation using an index system of 0 to 4, as follows:

0 = Practically no infestation.

1 = Slight infestation.

2 = Moderate infestation.

3 = Severe infestation.

4 = Very severe infestation.

From the data thus obtained, the average infestation per bush was calculated.

Red-spider abundance in relation to pruning and skiffing.

Red spider, as already noted, persists on some old leaves and janams of tea bushes during the cold weather but by clean pruning a great many of these leaves are removed and with them the mites. Assessment of red-spider infestation was made at Borbhetta in an experiment of randomised block design which consisted of two treatments (pruning *vs.* skiffing *) with eight replications, there being 98 bushes per plot (Table II).

TABLE II.

Incidence of red spider on pruned and skiffed tea at Borbhetta

Treatment	Date of operation	Date of observation	Red-spider infestation index (Mean of 8 replications)
Skiffed	14.iii.51	12-14.vi.51	3.63
Pruned	26.xii.50	12-14.vi.51	1.81
Critical difference at 1% level ..			1.11

Assessment was also made in two adjacent areas, one pruned and the other skiffed *, on a commercial estate in Cachar. Ten groups of 50 bushes each were examined, each group being selected at random from the inside of each area (Table III).

TABLE III.

Incidence of red spider on pruned and skiffed tea in Cachar.

Treatment	Date of operation	Date of observation	Red-spider infestation index (Mean of 10 replications)
Skiffed	10.i.59	2.vi.59	2.52
Pruned	16.i.59	2.vi.59	1.41
Critical difference at 1% level ..			0.25

* Skiffing means light skiffing unless otherwise stated.

It will be evident from Tables II and III that the pruned tea is less attacked than the skiffed tea. Harrison (1937) also concluded that tea left unpruned (skiffed) and carrying much old leaf and 'banjhi*' growth was especially susceptible to attack by red spider.

Skiffing or skiff pruning may be done in some cases to a few inches below the plucking level of the previous year. The effect of light and deep skiffing was assessed in two adjacent areas on a commercial estate in Cachar. Five hundred bushes in ten groups selected at random, each group with 50 bushes, were examined from the inside of each area (Table IV).

TABLE IV.

Degree of red-spider infestation on light and deep skiffed tea.

Treatment	Date of operation	Date of observation	Red-spider infestation index (Mean of 10 replications)
Light skiffed	20.i.59	4.vi.59	3.08
Deep skiffed	17.i.59	4.vi.59	1.98
Critical difference at 1% level ..			0.84

In light skiffed tea or in tea levelled off at the top, in which most of the leaves are left on bushes, the intensity of attack is higher than in deep skiffed tea, where comparatively more leaves are automatically removed during the operation.

Effect of time of pruning and skiffing.

The time of pruning has a definite influence on the incidence of red spider, and early pruned tea is more susceptible to red-spider attack than late pruned. The degree of red-spider infestation was assessed in early and late pruned teas in two adjacent areas on a commercial estate in Cachar. Five hundred bushes in ten groups selected at random, each group with 50 bushes, were examined from the inside of each area and the results are presented in Table V.

TABLE V.

Degree of red-spider infestation on early and late pruned tea.

Treatment	Date of operation	Date of observation	Red-spider infestation index (Mean of 10 replications)
Early pruned	12.xii.58	4.vi.59	2.66
Late pruned	29.i.59	4.vi.59	1.33
Critical difference at 1% level ..			0.24

Watt & Mann (1903) refer to a letter from a planter quoting that "late pruning (in April) will be the best remedy, or rather prevention for red spider attack: the bushes liable to it will get red spider on them before they are pruned, but pruning will remove a good deal, and the bushes will throw out shoots straight away without a check."

* Dormant shoot apex.

The main reason for this appears to be that early pruned bushes after producing new growth become banjhi, and the leaves become hard. As a result, the mites disperse to these leaves where they go on multiplying at an increased rate, while on late pruned tea they have to remain confined to old leaves until the new growth, which comes away much later, becomes hard enough for the mites to disperse. However, under congenial weather conditions, the build-up of the mite is so rapid that there may be little difference in the degree of attack on early pruned and on late pruned tea.

Harrison (1937) observed that "though early pruned tea is badly attacked by red spider, it is only that which has not been properly cleaned out that suffers severely, whereas the bushes which have been properly cleaned out by removing all 'banjhi' growth along with much of the old leaves are, however, less affected."

On the other hand, the time of skiffing has little influence on the mite attack. Five hundred bushes from inside of each area were examined (as in Table V) on an estate in the Dooars, and both early and late skiffed tea was found to be almost equally affected (Table VI).

TABLE VI.

Degree of red-spider infestation on early and late skiffed tea.

Treatment	Date of operation	Date of observation	Red-spider infestation index (Mean of 10 replications)
Early skiffed	15.xi.58	8.vii.59	2.47
Late skiffed	15.ii.59	8.vii.59	2.15

Red-spider abundance in relation to time of cleaning out.

Time of cleaning out did not show a significant influence on the incidence of red spider amongst the treatments (1) pruned and cleaned out on 7.xii.50, (2) pruned on 7.xii.50 and cleaned out on 21.i.51, and (3) pruned on 7.xii.50 and cleaned out on 14.iii.51, as assessed in a randomised block design experiment with three treatments and six replications, each plot having 84 bushes (Table VII).

TABLE VII.

Effect of time of cleaning out on red-spider incidence.
(Date of pruning, 7.xii.50.)

Date of cleaning out	Dates of observation	Red-spider infestation index (Mean of 6 replications)
7.xii.50	11-19.vii.51	1.06
21.i.51	11-19.vii.51	0.92
14.iii.51	11-19.vii.51	1.14

It may be mentioned that the whole area in which the experiment was carried out was less heavily attacked than usual in the year of observation.

Red-spider abundance in relation to degree of cleaning at pruning.

In top pruned tea, the degree of cleaning out varies from 'cut across', in which no cleaning is done, to 'stick pruning' which involves drastic removal not only of weak, but also of many strong, twigs. With different degrees of cleaning out, the quantity of old leaves removed from bushes also varies, and so also the population of red spider persisting on bushes, and the intensity of subsequent attacks.

The degree of red-spider infestation was assessed in an experiment at Borbhetta, in which different degrees of cleaning out were done. The lay-out of the experiment was a randomised block design with four treatments and four replications, there being 100 bushes per plot (Table VIII).

TABLE VIII.

Effect of degree of cleaning out on red-spider incidence.

Treatment	Red-spider infestation index (Mean of 4 replications)
Cleaning out banjhis, weak and crossing branches in alternate years (in the year of no treatment=control) ..	3.59
Cleaning out banjhis only (1)	2.68
Cleaning out banjhis, weak and crossing branches (2) ..	2.61
Cleaning out banjhis, weak and crossing branches at hand-breadth (3)	2.44
Critical difference at 1% level	0.71

Date of pruning, 22nd Dec. 1950 to 2nd Jan. 1951.

Date of cleaning out, 8th Jan. 1951.

Dates of observation, 22nd to 30th June 1951.

In the year of observations, 1951, the red-spider attack was severe in the experimental area and the plots in which (1) cleaning out banjhis only, (2) cleaning out banjhis, weak and crossing branches, and (3) cleaning out banjhis, weak and crossing branches at hand-breadth were done, were significantly less attacked than the plots in which 'no cleaning out' was done (Table VIII). Though there was no significant difference amongst the treatments 1, 2 and 3, the trend was that the more leaves removed at cleaning out the less was the attack.

Andrews (1928) observed that all processes which tend to bring about retention of poor and old wood in the bushes for a shorter or longer period caused an increase in the prevalence of red spider. Harrison (1937), from the results of observations on the red-spider incidence in relation to style of pruning, came to the conclusion that the tea that has been 'stick-pruned' is considerably less attacked by red spider than that receiving a lighter form of cleaning out, and the removal of banjhi growth of the previous season (together with a percentage of old leaves unavoidably removed at the same time) appears to be, as far as pruning operations are concerned, the chief factor in controlling red spider. Woodford (1947) observed that red-spider attack was associated with the degree to which the bushes were cleaned out: the more branches removed, the less the attack. He added that "the length of one year wood left at pruning was also associated with red spider attack. The least red spider occurred on the bushes pruned at the old pruning level, but the incidence of red spider did not increase with increasing amount of one year wood".

The degree of cleaning out as an important factor in reducing the red-spider incidence has been recognized for a long time, but how this reduction is effected was not exactly known. Since the red spider persists on a few old leaves and janams during the cold weather, that form of pruning and cleaning out which removes the greatest number of old leaves, including janams, is also the most effective in depleting the mite population persisting on bushes, and in thus reducing the intensity of subsequent attacks. Tea that has been thoroughly cleaned out is, therefore, less attacked than tea that has been merely cut across.

Red-spider abundance in relation to height of plucking.

Observations were made in a randomised block design carried out with treatments of different heights of plucking. The results show that plucking at different heights (4, 6 and 8 inches) above the pruning level has no effect on the red-spider attack. This confirms the findings of Harrison (1937) and Woodford (1947).

Red-spider abundance in relation to defoliation.

In districts which are subject to severe red-spider attack every year, complete defoliation of the pruned tea is often resorted to as a protection against future attacks. Assessment of the degree of infestation on pruned but not defoliated tea and also on pruned and defoliated tea was made in two neighbouring areas of a commercial estate in the Dooars. Five hundred bushes in ten groups selected at random, there being 50 bushes in each group, were examined from the inside of each area with the following results (Table IX).

TABLE IX.

Incidence of red spider on pruned and defoliated tea as compared with that on pruned but not defoliated tea.

Treatment	Date of observation	Red-spider infestation index (Mean of 10 replications)
Pruned on 22-28.xi.58 but not defoliated ..	13.vi.59	3.05
Pruned on 22-26.xi.58 and defoliated on 29.xi.59	13.vi.59	1.75
Critical difference at 1% level		0.39

It is obvious that the pruned tea which has been defoliated is significantly less attacked than the tea which has not been defoliated after pruning.

Further assessment was made on the effect of defoliation of pruned tea and compared with the incidence of the mite in light and deep skiffed tea from three neighbouring areas in another section of the same estate. The same number of bushes as in Table IX were examined in each case (Table X). The attack was, however, moderate in this part of the estate.

It is evident that the defoliated pruned tea is significantly less attacked than the light and deep skiffed teas which are not defoliated as a rule; there was, however, no significant difference in the degree of attack between the light skiffed and deep skiffed teas in this case.

Defoliation * means removal by hand of those old leaves which are left on

* Defoliation of tea by using chemicals is still under investigation of the Agricultural Branch. If it proves successful, without having any adverse effect on bushes, it may replace defoliation by hand.

bushes after pruning. Since janams also harbour some red spiders it is desirable that they be removed along with old leaves. Most of the mites thrown down with pruning and leaf-litter perish, and the very few mites that may climb up the bushes cannot re-establish themselves if there has been no bud-break at the time of defoliation. Defoliation is, therefore, done immediately after pruning and before bud-break takes place. Tea bushes cannot, however, be defoliated indiscriminately; they must be healthy and have sufficient food reserves in their roots. If necessary, the bushes must be given sufficient rest to build up reserves before they are pruned for defoliation, as defoliation may well have an adverse effect on bushes with low reserves, particularly if there is prolonged drought

TABLE X.

Incidence of red spider on pruned and defoliated tea as compared with that on light and deep skiffed but not defoliated tea.

Treatment	Date of observation	Red-spider infestation index (Mean of 10 replications)
Light skiffed on 10.ii.59 and not defoliated ..	3.vii.59	1.68
Deep skiffed on 27-29.i.59 and not defoliated	3.vii.59	1.51
Pruned on 17-23.xii.58 and defoliated on 23.i.59	3.vii.59	0.12
Critical difference at 1% level		0.98

after the bushes have exhausted all reserves in producing new growth. Harrison (1937) remarked that, if a bush has plenty of reserves, defoliation may do little or no harm, but it "may have serious effects on young tea and tea which is weak or low in reserves". It may be mentioned that defoliation of bushes after pruning encourages bud-break, and the defoliated bushes start flushing much earlier, but the ultimate effect on crop yield is not yet definitely known.

Partial defoliation leaving a few leaves at the top has not been effective in preventing an attack, as assessed in three neighbouring sections of an estate in the Dooars where four lots of 500 bushes, in ten groups of fifty, were examined after being given one of each of the treatments shown in the Table XI.

TABLE XI.

Effect of partial defoliation on red-spider incidence.

Treatment	Date of observation	Red-spider infestation index (Mean of 10 replications)
Deep skiffed on 15-16.xii.58 and not defoliated	6.vii.59	2.56
Pruned on 22-24.xii.58 and partially defoliated on 20.i.59	6.vii.59	2.34
Pruned on 19-20.xii.58 and defoliated on 10-14.i.59	6.vii.59	0.17
Critical difference at 1% level		1.03

Young infills which cannot be defoliated are focal points of the mite attack. It is, therefore, customary to treat these infills and one or two rows of bushes around them with acaricides to prevent the build-up of the mite population. Young laterals (branches arising from the lower part of the frame and which have not yet reached the pruning level) are also not pruned nor are they defoliated; they often carry red spiders and may be sources of infestation. They should, therefore, be treated as are the young infills. If this is not done, scattered bushes in defoliated sections are often found to be infested by red spider.

In a section prone to severe red-spider attack, defoliation of a small area may be of little advantage as there will be migration and transport of mites from the adjacent undefoliated areas of the section, unless the mite is thoroughly controlled in the latter. In one estate, 40 rows of bushes in one section were defoliated, leaving the rest of the section undefoliated. Assessment of the degree of attack was made on 200 bushes in ten replicates of 20 bushes each in both parts of the section. The results are presented in Table XII.

TABLE XII.

Degree of red-spider attack in defoliated and undefoliated pruned tea in a section where a small area was defoliated.

Treatment	Date of observation	Red-spider infestation index (Mean of 10 replications)
Pruned on 9-15.i.59 and not defoliated ..	13.vi.59	3.75
Pruned on 9-15.i.59 and defoliated on 20.i.59	13.vi.59	2.45
Critical difference at 1% level		0.80

From Table XII it is evident that though the defoliated area was significantly less attacked than the rest of the section which was not defoliated, the degree of attack was quite high even in the former, and the advantage usually gained from defoliation may be lost if only a small portion of a section is defoliated. Defoliation must be carried out over a large area to have its full effect.

Medium pruning *.—In medium pruned tea, many more leaves are removed during the operation than in normal pruning and in fact very few leaves are left except those on laterals arising from the lower part of the frame. Obviously the medium pruned tea is less attacked than any other type of pruned tea. In cases where the medium pruned tea is found to be badly attacked, the source of the attack can be invariably traced to laterals harbouring a great number of mites, or to adjacent badly infested areas.

Red-spider incidence on road-side bushes.

The bushes along the main roads, particularly those which become covered with dust, are severely attacked by red spider. The attack is most serious on two or three rows along the road and the degree of attack gradually decreases as the distance from the road increases. In view of this, ten rows of bushes along the main roads are defoliated as a safeguard against red-spider attack.

No explanation for the increased population of the mite on road-side bushes has yet been offered. In this connection, observations were made on pruned

* When the bush gets too high to pluck, it is cut back to 22-27" from the ground for efficient plucking.

tea on a neighbouring commercial estate in the cold weather. Five groups of five bushes each were selected at random in each of the rows listed in Table XIII from the side of the main road which remained covered by dust during the cold weather (Table XIII).

TABLE XIII.

Population of red spider on road-side bushes as compared with that on inner rows (in December).

Row number from the road-side	Average number of					
	Lateral branches per bush	Leaves including janams per bush	Infested leaves including janams per bush	Mites per infested leaf	Eggs per infested leaf	Mites including eggs per bush
After pruning but before cleaning out						
1st	12.4	260.4	18.6	15.4	16.5	591.8
2nd	8.7	180.4	12.6	9.9	13.2	291.5
3rd	8.2	148.0	11.5	8.0	11.0	216.0
10th	8.0	116.2	11.6	5.5	9.5	174.8
12th	8.3	107.0	12.0	5.4	8.0	158.7
After cleaning out						
1st	9.8	71.8	10.1	10.9	11.7	224.4
2nd	8.2	58.4	7.8	8.0	9.6	137.3
3rd	7.9	52.4	7.9	6.9	8.4	129.5
10th	7.7	57.8	7.8	6.3	8.5	115.0
12th	7.7	55.5	8.1	7.9	7.7	126.3

The results show that the lateral branches are more numerous on the first row of bushes along the road. Obviously, these bushes carry more old leaves and more red spider even after normal cleaning out.

Observations were also made on the incidence of Coccinellid predators of red spider on dust-covered bushes. Twenty-five bushes in five groups of four each were examined in each row from the first to the ninth row from the road-side (Table XIV).

The adults and larvae of Coccinellid predators (*Verania vineta* Gorham, *Stethorus* sp., *Jauravia* sp. and *Scymnus* sp.; vide Das, 1959b), were virtually absent on a few rows (first to fourth) from the road-side which remain almost

TABLE XIV.

Incidence of Coccinellid predators on dust-covered road-side bushes.

Row number from road	Average number of predators per bush
First	0.00
Second	0.00
Third	0.00
Fourth	0.05
Fifth	3.37
Sixth	1.25
Seventh	1.45
Eighth	6.00
Ninth	4.58

completely covered with dust, as compared with the inner rows (eighth and ninth) which are away from the road and are less covered with dust.

From the Tables XIII and XIV, it is apparent that the presence of a greater number of laterals on road-side bushes, harbouring more red spiders during the cold weather, and the lower prevalence of predators on dust-covered bushes are at least in part responsible for the increased abundance of red spider on road-side bushes, but it is also possible that the stimulating effect of inert materials may be a further factor contributing to the abundance of the mite on these bushes. Fleschner (1958) recorded a higher population of mites on terminals of *Citrus* plants treated with non-toxic materials such as talc, road dust and zinc-deficiency spray material, and he concluded that this increase was due to a direct stimulating effect of inert residues on mites. According to Holloway, Henderson & McBurnie (1942) "the increase of citrus red mite associated with the use of inert spray materials was due to the characteristics of the materials, not to influences of biological control factors".

Red-spider abundance on abandoned tea and tea seed-trees.

Abandoned tea * is severely attacked in the first year after abandonment and to a lesser degree in the second year. As the plants grow bigger, the degree of infestation progressively decreases until it is only slight, if present at all, and confined to plants at the border of the garden. In tea seed-gardens the red spider is virtually absent except on border trees which occasionally may be very slightly attacked.

The reason for almost total absence of red spider in seed-gardens where the tea plants are allowed to grow about 20 ft. high is not well understood. The red spider does not normally occur on young seed-trees above a certain height, about 5 ft. from the ground level. In old seed-gardens the sun can scarcely penetrate into the interior, and the lower part of the trees, which remains shaded, is almost always free from red spider. It may be mentioned here that shaded tea is always less attacked than that in the open. If shade is assumed to be responsible for the absence of red spider inside the seed-garden, it is not clear why border trees, particularly those on the south and south-west, which are exposed to the sun, should not be as severely attacked as the skiffed tea.

Summary.

The red spider, *Oligonychus coffeae* (Niet.), persists in all stages of its development on a few old leaves and 'janams' (small leaves at the base of the shoot) of tea bushes during the cold weather, and this persisting population is primarily responsible for the attack in the spring.

In pruning, a great many of the old leaves (including janams) are removed from bushes, and, concomitantly, the red spider. Pruned tea is, therefore, less attacked than unpruned tea or 'skiffed' tea (where just a little is cut off the tops of the shoots) in which comparatively more leaves are left on bushes.

Early pruned tea is, however, more subject to red-spider attack than late pruned tea, but there is little difference between early and late cleaning out (removal of dead snags, weak and crossing branches, etc.), and also between early and late skiffing, in their effect on the degree of red-spider attack.

The degree of cleaning out has a direct influence on the incidence of red spider. The more leaves removed at cleaning out the less is the attack. Obviously, that form of pruning and cleaning out which removes most old leaves will correspondingly most reduce the intensity of attack.

* Tea may be abandoned temporarily when it is due to be uprooted, but uprooting may be delayed for some reason or other. Uneconomic areas that are not suitable for replanting may also be abandoned.

Tea which has been defoliated as a preventive measure against subsequent attacks remains practically free from the mite. Medium pruned tea, from which almost all leaves are automatically removed during the operation, remains almost free from attack, as after defoliation.

Young laterals of pruned bushes are usually not defoliated, nor are young infills, and they may be sources of infestation; but it is customary to treat them with acaricides to prevent the spread of attack.

Different heights of plucking have no observable effect on the red-spider attack.

Bushes along the main roads which become covered with dust are severely attacked by red spider. This increase appears to be mainly due to the presence of more laterals carrying more mites on the first row by the side of the road, and also to the lower incidence of predators on dust-covered bushes during the cold weather.

Abandoned tea is severely attacked in the first year after abandonment, but as the trees grow larger the degree of attack progressively decreases. In tea seed-gardens, the red spider is virtually absent, except that a slight infestation may occasionally show up on border trees.

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References.

- ANDREWS, E. A. (1928). Red spider.—*Quart. J. Indian Tea Ass.* **1928** pp. 206–219.
- COMRIE, L. C. (1939). Proceedings of the Third Annual Conference, Indian Tea Association, pp. 13–14.
- DAS, G. M. (1959a). Problems of pest control in tea.—*Sci. & Cult.* **24** pp. 493–498.
- 47 364 DAS, G. M. (1959b). Bionomics of the tea red spider mite, *Oligonychus coffeae* (Nietner).—*Bull. ent. Res.* **50** pp. 265–274.
- FLETSCHNER, C. A. (1958). Field approach to population studies of Tetranychid mites on *Citrus* and avocado in California.—*Proc. 10th int. Congr. Ent.* **2** pp. 669–674.
- HARRISON, C. J. (1937). The occurrence and treatment of red spider on tea in north east India.—*Memor. Tocklai exp. Sta. Indian Tea Ass.* no. 2, 26 pp.
- HOLLOWAY, J. K., HENDERSON, C. F. & MCBURNIE, H. V. (1942). Population increase of *Citrus* red mite associated with the use of sprays containing inert granular residues.—*J. econ. Ent.* **35** pp. 348–350.
- WATT, G. & MANN, H. H. (1903). The pests and blights of the tea plant.—2nd edn., 429 pp. Calcutta.
- WOODFORD, E. K. (1947). Factors effecting the distribution and intensity of the attack of red spider (*Tetranychus bioculatus* W.M.) at Borbhetta in the spring of 1947.—*Rep. Indian Tea Ass. Sci. Dep.* 1947 appdx. 1.

THE CONTROL OF FRIT FLY, *OSCINELLA FRIT* (L.), IN SWEET CORN
(*ZEa MAYS*) BY THIMET (O,O-DIETHYL S-ETHYLTHIOMETHYL
PHOSPHORODITHIOATE).

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Sweet corn (*Zea mays*) is being grown on an increasingly large scale in southern England, for direct consumption and for the preparation of deep-freeze products. Modern commercial sweet corns are produced each year by hybridisation, the most popular varieties being Golden Early, John Innes hybrids and North Star—the last mentioned is especially suited for modern deep-freezing techniques. These hybrids are more vigorous, higher yielding, and more uniform than the older open-pollinated varieties. They mature in the following order, Golden Early, John Innes hybrids and North Star—the earlier the variety the smaller the cob.

Sweet corn is almost invariably severely attacked by the frit fly, *Oscinella frit* (L.) (Diptera, CHLOROPIDAE), and a large proportion of the young plants is affected. The larvae and pupae of the fly are present in early spring in alternate wild grass hosts in the absence of its favoured cultivated host—spring-sown oats. The control of the frit fly is probably obligatory, since sweet corn has to be sown during the period 1st–20th May, the appearance of the seedlings thus coinciding in normal years with the spring flight peak of the fly (15th–30th May).

Goodliffe (1942) recorded larvae of *O. frit* on young shoots of sweet corn, accompanied or followed by *Aphanotrigonum trilineatum* (Mg.) and *Elachiptera cornuta* (Fall.), which were presumably feeding on the detritus produced by them. As many as 20 frit-fly larvae have been found in one plant of tillering maize by Newton (1935).

Visible symptoms only appear, according to Böning (1952), if more than four larvae are present in the one shoot. With respect to southern England at least the authors find that visible symptoms will appear even with a single larva present, possibly because growth is relatively slow in this country until July.

One result of frit-fly attack is that very often both male and female inflorescences are found in the same sheath (Löhle, 1930), and this has been confirmed with several plants in these experiments.

On the Continent, where the chief demand is for fodder and silo maize, the frit-fly problem has recently been summarised by Nolte & Fritzsche (1959) in eastern Germany, and Karpova (1958) describes the relative development of attacks by *O. frit* and the closely allied *O. pusilla* (Mg.) in maize in the Soviet Union.

In grain varieties and especially sweet corn there is a loss both in yield and quality associated with a reduction in the number of marketable cobs, and stunting of the cob. Batygin & Shapiro (1956) used two sprays of γ BHC, the first at the 1- to 2-leaf stage and the second 5–7 days later. Kalashnikov & Shapiro (1958) obtained control with chlordane, dieldrin, γ BHC (but not DDT)—but Thomas (1958) reports the best control on oats with DDT sprays. Haskell (1951) also suggests the dusting of the rows of young plants with DDT.

The current recommendation for the protection of sweet corn in this country was evolved by Dawson (1955) in collaboration with one of us (W. F. J.). It

consists of a timed row drench of a dieldrin emulsion made from Dieldrex 15, 15 per cent. emulsion concentrate, using $1\frac{1}{2}$ pints/100 gal. water, the drench being applied in a narrow band on top of the seedlings as they come through the soil, and again 7–10 days later. About 250–300 gal./acre are usually required.

The present work was carried out in connection with parallel small field-plot experiments in the early protection of spring oats by the use of seed dressings and granular formulations of various insecticides. Since seed treatment, and seed-furrow and row applications of granular Disyston (O,O-diethyl S-2-(ethylthio)ethyl phosphorodithioate) had proved disappointing (Armstrong, 1958), it was decided to try the newly available 8 per cent. granular formulation of Thimet (O,O-diethyl S-ethylthiomethyl phosphorodithioate), in different methods of application.

Brown (1957) found that 0.1–0.5 part per million Thimet has to be maintained in the tissues to give satisfactory control of the Hessian fly, *Mayetiola destructor* (Say). Thimet works through the roots and stem rather than through the leaves (Thimet Technical Manual) and it therefore seemed well suited to combat frit-fly attacks.

The application of spray or dust treatments a certain number of days after sowing cannot always give control of stem borers in graminaceous crops each year under varying climatic conditions. A more flexible system of timed spraying, depending on biological events adjusting themselves to climatic change, would involve a complete knowledge by the grower of the phenology of the fly combined with that of the sweet-corn crop. However, by placing the toxicant in the seed furrow, it was hoped to eliminate the need for this careful timing. Seed treatments with 44D Thimet on activated charcoal with methyl cellulose has delayed germination, stunted growth, and reduced the stand significantly in controlling the Hessian fly in wheat (Guyer, Brown & Wells, 1958) and in the treatment of seed cotton (Hopkins, Fye & Walker, 1958). This method of treatment was therefore omitted in the present work.

Material and methods.

It was decided to try the application of 8 per cent. granular Thimet by hand in the seed furrow at sowing time, in row placement on the newly emerged plants, and broadcast over the beds, all at the rate of 2 lb. of active ingredient per acre. Distribution was effected by dilution with silver sand (3:1). Great care is necessary in handling and in the avoidance of inhalation of the material, although the granular formulation produced a minimum of dust.

The experiment was laid out at Silwood Park, Sunninghill, Berks., on a light, loamy sand, which was slightly acid in reaction.

pH 6.8	{ Organic matter	4%
	{ Clay	7.5%
	{ Sand	87.4%—various grades.

The field plots (10 ft. \times $6\frac{1}{2}$ ft.) were laid out in a 4×4 Latin square with the plots split and randomised for two sowing dates (6th and 13th May). Two seeds were sown together every 6–9" in furrows drawn out to $1\frac{1}{2}$ –2" in depth and just showing moist soil. The seed supplied by a commercial grower had been treated with captan (N-(trichloromethylthio)-4-cyclohexene-1,2-dicarboximide) and Thimet has given good compatibility with it. The furrows were covered in and the soil was compacted. Emergence of the seedlings took place 9–10 days after sowing.

At a later date, 6 cwt. of complete fertiliser (Fison's 45) was placed in bands between the rows and raked into the surface soil. The rows were the standard 2 ft. apart; the plants were later singled to 9 in. apart after the count of affected

plants had been made. This was, of course, nearly twice the recommended final plant density and with the exceptionally dry growth conditions may have affected the final yield, although excellent marketable cobs were produced in sufficiently large quantities for taint and palatability estimations. The assessment of results was made on the number of damaged plants and the final yield of cobs. Counts of plants showing deadhearts and other abnormal conditions were made visually, supported by dissections to determine the cause of certain observed distortions of the shoots and leaves.

The harvesting of the cobs was carried out from 21st August–5th September, the criteria of ripeness being that the cobs matured about 4–5 weeks after the silks appeared—when the silks were brown and withered, the pale yellow cobs were plumb inside the sheaths, and the grain was milky. The cobs were weighed complete with sheaths as harvested to give a yield assessment figure. In each plot of the best treatment (B, see Table I) 16 large cobs were selected (approx. 24 lb.) and another 16 from the bulked controls. These were submitted for immediate deep-freezing and subsequent determination of Thimet residues and tasting tests.

The percentage of infested plants and final yield of cobs associated with the various treatments are shown in Table I.

Observations on the damage to young plants by *O. frit*.

Damage to young plants by frit fly has been known to growers of sweet corn who may not always have been aware as to its cause. Dawson (1955) has described and illustrated the principal damage facies. Frit flies were observed to assemble on the young plants as soon as the first leaf was expanded. Eggs were observed in the same positions as on oats, namely under the coleoptile, beneath the leaf sheath, and outside the coleoptile at soil level, or at most $\frac{1}{4}$ in. below the surface. Eggs were rarely seen in the soil away from the plant, and it must be stressed that *O. frit* is not normally a soil insect. The egg peak extended over several days—15th–25th May—and by 18th June distortion of the young plants and death of the primary shoots were noticed. The larvae on hatching seemed to bore into the shoot at about $\frac{1}{2}$ – $\frac{3}{4}$ in. above the soil. They fed on the central tissues and bored in a spiral path down to the growing point. The growing point was reached in 1–3 days, producing visible symptoms without delay, in the form of a deadheart.

In many cases, however, the larvae went in the opposite direction and were found at the tip of the shoot. The brown, frass-stained, dead tissue was very evident but the primary shoot was often not killed out, although growth was nevertheless stunted.

Three other abnormal conditions may be observed:

1. Stunted growth and a twisting or deformation of the first six leaves. The leaves often have elongate, brown lacerations, and are frequently rolled together at the tips; this is due to the larvae feeding on the whorled leaves before they are unrolled and expanded.
2. Leaves are bent over and may be rolled together at the tips, being at first sticky and then dry and brown. The developing shoot in some cases may penetrate this arched leaf structure (cf. 'pokka boeng' of sugar-cane, caused by a fungus). At both Silwood Park and at Oxford this condition was observed, giving every appearance of a frit attack. However, on dissecting about 100 of the plants there was no trace of larvae or any evidence of internal boring. E. S. Bunting (personal communication, 1959) has suggested that this may be a physiological disturbance, and similar symptoms have been reproduced in the laboratory under certain conditions of temperature and humidity.

3. The deadhearted primary shoot is replaced by anomalous tillering from the base of the plant. These tillers are also attacked, but to a much lesser extent, by newly hatched larvae, or by larvae migrating from the attacked primaries.

Healthy plants are vigorous, sturdy and quick-growing, each plant having a light-green leaf emerging from the centre, indicating that the growing point is undamaged.

Once a plant has made 5-6 leaves it is said to be practically immune to attack (Dawson, *loc. cit.*). However, outside the experimental plots a few plants of John Innes hybrids which had been grown to the 5-leaf stage under glass until 12 in. tall, were planted out, and these were attacked.



Fig. 1.—Damage to young sweet corn by *Oscinella frit*. Fore-ground: grass-like appearance of untreated plants contrasted with taller single-stemmed plants protected with Thimet. Heavily attacked Blendra oats in background.

On the Continent, wireworms can cause symptoms like those of frit fly, due to their entry at the base of the plant where they feed on the young rolled leaves (Schlumberger, 1937). The result of attacks by *O. frit* can be seen in fig. 1 in which the grass-like appearance of the attacked plants may be compared with that of the single primary shoot of the normal ones.

Experimental results.

The percentage germination on all plots was very high, in excess of 90 per cent. The seed-furrow treatment had no effect on germination or hybrid vigour, and there was no reduction in the stand. The great majority of plants treated in this way were quite normal; a few, however, on the various treated plots showed a slight yellowing of the first leaves but this disappeared after 7-10 days.

Similarly with the row placement, but not the broadcast treatment, a slight initial wilting appeared in a few plants, but they recovered very quickly. Some treated plants tended to show a slightly faster growth rate than the majority; this continued up to the 5-leaf stage, after which equalisation was rapid, and there was no difference in the final yields.

Thimet granules in the seed furrow probably release the toxicant more slowly than as a row placement or broadcast, thus prolonging its effectiveness.

In young plants, especially of the first sowing date, the granules in the row-placement and broadcast treatments formed noticeable deposits at the base of the funnel of the young plants.

The attack on the shoots reached a maximum in the last week in May but waned in early June and although the second (panicle) generation of flies emerged on 20th June, no further damage was done either to the main shoots or floral organs.

In computing the results of the experiment it was decided to combine the figures for the two sowing dates (6th and 13th May) since the differences in infestation and yield were negligible (Table I).

TABLE I.

Results of Thimet applications to sweet corn against *Oscinella frit*.

	Per cent. infested plants (angles)	No. of cobs per whole plot	Yield of whole plot (kg.)	Cob weights (g.)
A	14.0	60.0	11.37	180.5
B	3.8	63.5	12.52	180.3
C	3.5	51.8	9.49	180.0
D	44.9	38.7	5.94	155.1
SE	± 3.04	± 0.86	± 1.13	± 13.2
LSD	10.5	3.0	3.9	6.3
$P = 0.05$				

Sown 6th and 13th May 1959, in a 4 × 4 Latin square.

Treatments A = 8% Thimet granules broadcast on surface
 B = 8% Thimet granules placed in seed furrow
 C = 8% Thimet granules applied as a row placement
 D = Untreated control.

{ All at rate of 2 lb. actual
 Thimet per acre in 3:1
 dilution with dry silver
 sand.

These figures show clearly the significant effect of all the treatments compared with the untreated plots. The data were insufficient to establish a regression of yield on percentage infestation but it is evident that the crop was more than halved by the naturally occurring infestation of 45 per cent. of the primary shoots. The best protection was afforded by the row placement and the furrow treatments, although the yield from the former (C) was lowered owing to a severe soil gradient which affected the lower corner of the Latin square under the dry conditions of the 1959 summer. The infestation of the broadcast treatment (A) was significantly more than that of the furrow treatment (B) although this is not reflected in the

final yield. In the untreated control, the number of cobs was severely reduced by the infestation, and the mean cob weight was 14 per cent. lower. The general level of infestation by *O. frit* in this season, as measured by the percentage of deadhearts (42.7%) in an adjacent standard sowing of Blenda oats, was slightly higher than normal for the area (*ca.* 30%).

The application of the insecticide into the seed furrow offers a new approach to the frit-fly problem on sweet-corn seedlings. However, before a practical recommendation could be made the following points must be considered.

1. Residues on cob.
2. Taint.
3. Soil accumulation.
4. Effect on soil microbiology.

The results of the estimation, by the anticholinesterase method*, of the Thimet residues present in the cobs taken from each replicate of the seed-furrow treatment (B), were as follows:

S1 = 0.011	} p.p.m. Thimet oxygen analogue sulphone.
S2 = 0.014	
S3 = 0.015	
S4 = 0.028	

The figure for the analogue should be multiplied by two to give the equivalent in terms of actual Thimet. Even when this is done there is still only a very minute trace of toxic material present and in the region of 50 times less than a reasonable tolerance figure of 1 p.p.m. (for potatoes). Tasting tests were carried out by a panel of six persons on a number of cobs harvested and immediately deep-frozen, after a period of three months, but no detectable taint was reported by the panel.

Casual observations tended to show an increase in Aphids and thrips on the untreated maize plants after about 5-6 weeks, although no counts were made.

We may therefore conclude that the use of Thimet in a granular formulation applied either as a seed-furrow or a row placement may be a useful addition to the standard method of dieldrin spraying, provided that the operator is fully aware of the ordinary precautions necessary when using a toxic material.

Summary.

Sweet corn (*Zea mays*) is frequently attacked by *Oscinella frit* (L.) in southern England because the optimal sowing date (1st-20th May) determines the appearance of the seedlings at the peak of the spring flight (13th-30th May).

A Latin-square experiment including three Thimet treatments and controls showed that almost complete protection could be given by seed-furrow and surface placements along the rows of an 8 per cent. granular formulation at the rate of 2 lb. actual Thimet per acre.

The crop on the untreated control plots was more than halved by the naturally occurring infestation of 45 per cent. of the primary shoots.

Estimation of Thimet residues in cobs taken from the seed-furrow treatment showed that only a very minute trace of toxic material was present.

Tasting tests on cobs from treated plots revealed no detectable taint.

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We should like to thank Mr. Fraser and Mr. B. H. Bagnall for their interest throughout the experiment and for their help in growing the crop and in arranging the residue determinations and the tasting tests.

* The analysis was done by the Murphy Chemical Co., Ltd., Wheathampstead, Herts.

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References.

- ARMSTRONG, K. (1958). Experiments in the control of the frit fly.—D.I.C. thesis, Imperial College.
- BATYGIN, N. F. & SHAPIRO, I. D. (1956). Fritfliege—ein gefährlicher Mais-schädling. [*In Russian.*]—*Kukuruz* **1** no. 3 pp. 42–45.
- BÖNING, K. (1952). Krankheiten und Schädlinge an Mais.—*Pflanzenschutz* **4** pp. 103–107.
- BROWN, H. E. (1957). Hessian fly control with systemic insecticides.—*FAO Plant Prot. Bull.* **5** pp. 149–155.
- DAWSON, C. D. R. (1955). Pests can ruin your sweet corn.—*Nurserym. & Seedsm.* **120** pp. 1186–1188.
- GOODLIFFE, F. D. (1942). Studies on insects bred from barley, wheat, maize and oats.—*Bull. ent. Res.* **32** pp. 309–325.
- GUYER, G. E., BROWN, H. M. & WELLS, A. (1958). An evaluation of systemic insecticides for control of hessian fly in Michigan.—*Quart. Bull. Mich. agric. Exp. Sta.* **40** pp. 595–602.
- HASKELL, G. (1951). Studies with sweet corn. The frit fly problem.—*Bull. ent. Res.* **42** pp. 519–526.
- HOPKINS, A. R., FYE, R. E. & WALKER, R. L. (1958). Field tests with Thimet and Bayer 19639 for cotton-insect control.—*J. econ. Ent.* **51** pp. 100–102.
- KALASHNIKOV, K. E. & SHAPIRO, I. D. (1958). The most effective measures of control of pests and diseases of maize. [*In Russian.*]—*IX Mezhd. Konf. Karant. Zashch. Rast.* 1958 repr. 15 pp.
- KARPOVA, A. I. (1958). Some features of development and injuriousness of frit-flies (*Oscinella pusilla* Mg. and *O. frit* L.) on maize in non Chernozem regions. [*In Russian.*]—*Rev. Ent. URSS* **37** pp. 812–819.
- LÖHLE, M. (1930). Beobachtungen über Aenderungen im Habitus an von Fritfliegen befallenen Maispflanzen.—*Z. PflKrankh.* **40** pp. 137–143.
- NEWTON, H. C. F. [1935]. Insect pests at Rothamsted and Woburn, 1933–4.—*Rep. Rothamsted exp. Sta.* 1934 pp. 71–73.
- NOLTE, H. W. & FRITZSCHE, R. (1959). Beobachtungen über Maisschädlinge im Sommer 1958.—*Dtsch. Landw.* **10** pp. 116–118.
- SCHLUMBERGER, O. (1937). Über Fritfliegen- und Drahtwurmschäden beim Mais.—*Angew. Bot.* **19** pp. 153–157.
- THOMAS, J. D. (1958). Control of frit fly by chemical means.—*Ann. appl. Biol.* **46** pp. 497–501.

A NOTE ON *GLOSSINA MEDICORUM* AUST. (DIPTERA) IN GHANA.

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L.C.

(PLATE XII.)

While I was working at the Biological Research Institute, University College of Ghana, a few observations were made on the tsetse fly, *Glossina medicorum* Aust. Although the observations are very incomplete it is considered worthwhile to record them because of the very few data which are available on this species.

Method of collecting.

It was found that *G. medicorum* was readily attracted to a vehicle, in this case a Land-Rover, moving through the bush at about 5 m.p.h. Flies which came into the vehicle were trapped by closing the windows and then caught in tubes or small nets. *Glossina palpalis* (R.-D.) and *G. longipalpis* Wied. were also taken by this method, coming to the vehicle even when it was not moving. *G. medicorum* was not attracted to a stationary vehicle, nor did it normally attack man, and only four specimens out of over 400 collected were seen to bite a man. Nash & Davey (1950) also record that *G. medicorum* only rarely attacked man and they collected this species by searching for it at rest. This method could not be used in Ghana because of the difficulty of penetrating the thicket. No specimens were taken in traps.

The sex ratios of the three species of tsetse flies collected in the Land-Rover are given in Table I. In all the species approximately equal numbers of the two sexes were collected.

TABLE I.

Sex ratios of the *Glossina* spp. collected in a Land-Rover at Ofankor.

Species	Number collected	Sex ratio M/F
<i>G. medicorum</i>	406	0.91
<i>G. palpalis</i>	88	1.32
<i>G. longipalpis</i>	182	0.72

Locality.

The collections were made near the village of Ofankor, about 11 miles north of Accra. From the village, a track, just passable to the Land-Rover, led up the side of a hill, the lower slopes of which were covered in dense secondary thicket. This was rarely more than 15 ft. high, consisting largely of *Fagara xanthoxyloides* and *Pavetta corymbosa*, and did not include any big trees. Each year parts of the thicket were cleared for planting maize and cassava, but after one year no more maize was planted and the remaining cassava became swamped by herbs and young shrubs. Ultimately the shrubs became dominant again and the area became continuous with the surrounding thicket.

8140

Higher up the hill the thicket was intersected by small areas of low grass which became progressively more extensive until, near the top of the hill, the thicket was reduced to isolated clumps in a general area of grassland. Where the thicket began to open out (Pl. XII, fig. 1) it was composed of a few small trees such as *Elaeophorbia*, *Parkia* and *Antiaris africana*, rarely much over 20 ft. high, and the same shrubs as lower down.

At the top of the hill the thicket only occurred in small clumps and as isolated shrubs of *Malacantha alnifolia* and *Crossopteryx febrifuga*, growing to a height of four or five ft. (Pl. XII, fig. 2). The grassland areas on the upper parts of the hill did not appear to be maintained as such by cultivation since this was restricted to the lower slopes. Their apparently permanent character may partly have resulted from the annual fires which swept the area, largely preventing the regeneration of shrubs.

The thicket or thicket clumps were dense on the edges but there was very little undergrowth within the stand and, although the shrubs formed a tangled mass above, at ground level the stems were generally well separated. The thicket thus appeared to provide a suitable resting and breeding ground for *Glossina* while the grassy open spaces provided the feeding grounds. In this connection it is significant that while *G. medicorum* was taken all along the track, from the dense thicket to the almost continuous grassland, it was most commonly collected where the thicket first began to open out.

This habitat of *G. medicorum* is of particular interest because of the complete absence of big trees. This species has previously been regarded as a high-forest species (Nash & Davey, 1950) although, in Ghana, Morris (1934) recorded it in transition forest with, apparently, only a few large trees remaining, and, recently, Page (1959) in Nigeria has described its occurrence in forest patches on the edge of savannah. Page suggests that *G. medicorum* occupies a drier habitat than other members of the group of species related to *G. fusca* (Wlk.) and this certainly appeared to be true in Ghana.

Distribution.

G. medicorum was taken at several places near to Accra, always in the belt of secondary thicket which extends from Takoradi in the west almost as far as the Volta River in the east (see Nash, 1948, Gold Coast map no. 2 "secondary coastal thicket"). Morris recorded this species close to Takoradi and it is probable that it occurs throughout the thicket, wherever suitable feeding grounds are available. In view of the local abundance of this species, on one occasion over 50 were collected in the Land-Rover in an hour, and the fact that it appears to be a potentially dangerous vector of trypanosomes (Nash, 1959; Page, 1959), it is clear that it might be a danger to any scheme to introduce cattle into those parts of the Accra plain adjacent to the thicket.

Food sources.

On the hill at Ofankor there were no domestic animals but game animals were not uncommon, although rarely seen. The following is a list of animals observed in or near the area by the late Mr. A. H. Booth.

Spot-nosed monkey
African civet
Egyptian mongoose
White-tailed mongoose
Forest genet
Bush-pig

Bushbuck 48 157
Black duiker
Maxwell's duiker
Red-flanked duiker
Royal antelope

To judge from the spoor which were observed, bushbuck were the most common animals, and recent work in Nigeria (Nash, 1959) suggests that bushbuck

and members of the SUIDAE are the most important sources of food for *G. medicorum*.

Daily and seasonal activity.

Regular monthly collections of flies were made but they were standardised only in that the same stretch of track was sampled for the same period of time on each occasion. Much larger numbers of flies were collected just as it was getting light (about 0600 hr.) than between 0800 and 0900 hr. and later still only very small numbers were taken. Nash (1952) recorded this species as being active during the twilight hours rather than at other times and has recently suggested (1959) greater activity in the early morning than in the late evening.

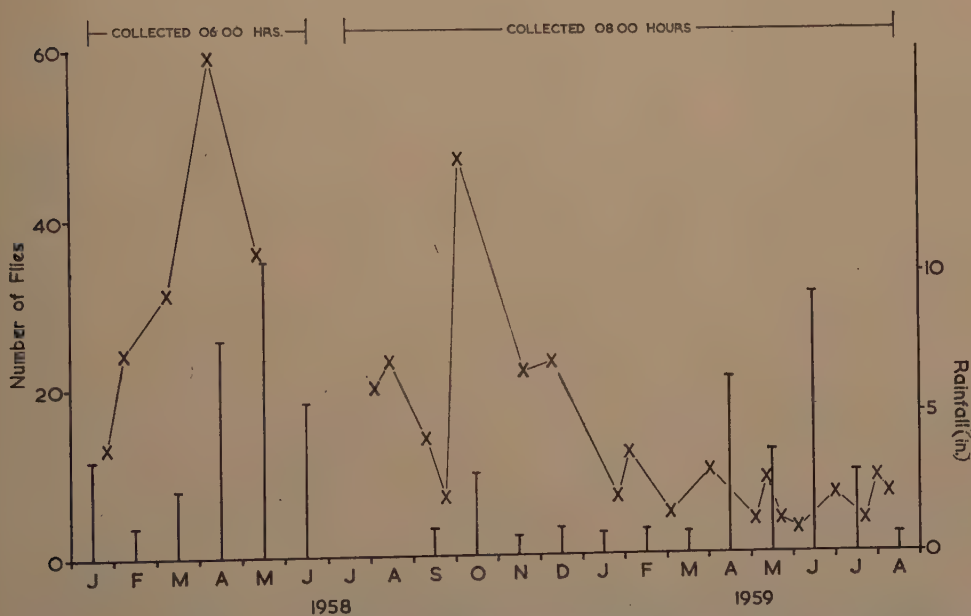


Fig. 1.—The numbers of *G. medicorum* collected at each visit and the total monthly rainfall.

The numbers of *G. medicorum* collected on each visit to Ofankor are given in fig. 1. From January to May 1958 all the collections were made at 0600 hr. but after this they were made at 0800 hr. Thus the actual numbers of flies collected in the first period are not comparable with those in the second, but the trends, increases or decreases, probably are. The greatest numbers of flies were collected in April and October 1958 with minima in January and September. This suggests an association between the abundance of flies and rainfall but there were no comparable fluctuations in the early part of 1959. There was also a suggestion of a relation between numbers of flies and saturation deficit but the sampling methods do not warrant a closer inspection of the data.

Size.

As an indication of the size of the flies, measurements were made with a micrometer grid of the centre part of the fourth longitudinal vein as described by

Jackson (1946). The figures given for 1958 are more reliable than those for 1959 because the samples were larger, but in both years and in both sexes the trend was similar (fig. 2). In the early months of the year the flies tended to decrease in size, reaching a minimum in February. After this they increased slightly in size but in May the flies were smaller than at any other time. Then they became bigger again, the males reaching a maximum size in August 1958 and the females in October while a comparable increase in size was observed in July and August 1959. Towards the end of the year the flies again became smaller.

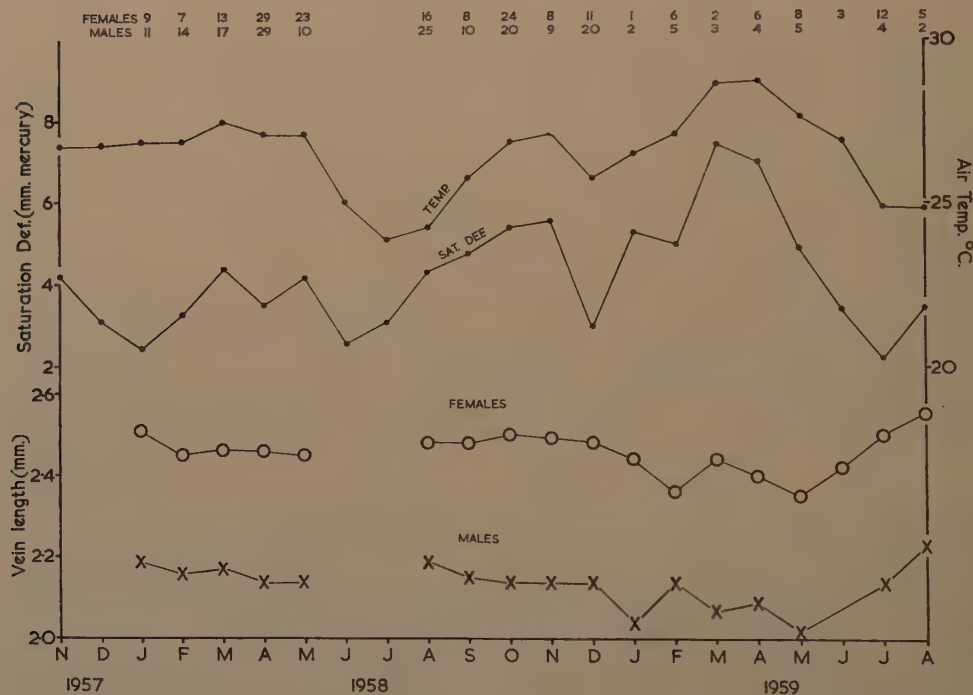


Fig. 2.—Seasonal variation in the size of *G. medicorum* at Ofankor (expressed as the length of the middle part of the fourth longitudinal vein) and the mean monthly saturation deficit and air temperature at 0900 hr. (Meteorological data from Pokoase Agricultural Research Station about 1 mile from Ofankor.) Numbers at the top of the figure give the number of measurements on which each point is based. No flies were collected or measured in June or July 1958.

It is noticeable that the flies collected in the first six months of 1959 were smaller than those from the corresponding period of 1958 and this may be related to the very dry conditions prevailing at the end of 1958 and beginning of 1959. Size was negatively correlated with the saturation deficit of the two previous months, that is, with the conditions experienced by the parent flies and the puparia (Table II). Thus small flies followed a period of high saturation deficit and larger ones a period of low saturation deficit. It will be seen from fig. 2 that the fluctuations in saturation deficit were rather greater in the first half of 1959 than they were in the same period of 1958 and the fluctuations in

size were correspondingly larger. These larger fluctuations in size might be regarded as resulting from the small numbers measured during this period but the fact that the variation showed similar trends in both males and females suggests that the fluctuations were real and not the result of the small samples. There was no correlation of size with the saturation deficit three months before nor with air temperature at any time, except possibly for male size with the mean temperature of the previous month.

TABLE II.

Correlations of size in *G. medicorum* with mean monthly temperature and saturation deficit.

	Month	Sex	Correl. coeff.	Student's <i>t</i>	Significance
Saturation deficit	previous	M	- 0.70	3.80	$0.01 > p > 0.001$
		F	- 0.59	2.92	$0.01 > p > 0.001$
	2 before	M	- 0.75	4.40	$0.001 > p$
		F	- 0.62	3.16	$0.01 > p > 0.001$
	3 before	M	- 0.34	1.41	$p > 0.1$
		F	- 0.27	1.21	$p > 0.1$
Temperature	previous	M	- 0.54	2.50	$0.05 > p > 0.01$
		F	- 0.29	1.34	$p > 0.1$
	2 before	M	- 0.47	2.08	$0.1 > p > 0.05$
		F	0.10	0.42	$p > 0.1$

Summary.

Glossina medicorum Aust. was collected in considerable numbers in thicket near to Accra, Ghana. The habitat was unusual in that the thicket rarely exceeded 15 ft. in height and big trees were entirely absent. Grassy open spaces within the thicket provided the feeding grounds and a list of possible hosts is given.

There was some suggestion of an association between the abundance of flies and the rainfall in 1958 but not in 1959, while the size of the flies was inversely correlated with the saturation deficit.

Acknowledgements.

I am indebted to Dr. T. A. M. Nash for pointing out the significance of the Ofankor habitat and for confirming that specimens of *G. medicorum* from this habitat were typical. Dr. J. K. Morton kindly identified the plants referred to and Mr. Gabriel Dza assisted in the collection of the samples.

References.

- JACKSON, C. H. N. (1946). An artificially isolated generation of tsetse flies (Diptera).—*Bull. ent. Res.* **37** pp. 291–299.

- 45 107
- MORRIS, K. R. S. (1934). The bionomics and importance of *Glossina longipalpis*, Wied., in the Gold Coast.—*Bull. ent. Res.* **25** pp. 309–335.
- NASH, T. A. M. (1948). Tsetse flies in British West Africa.—77 pp. London, Colon. Off., H.M.S.O.
- NASH, T. A. M. (1952). Some observations on resting tsetse-fly populations, and evidence that *Glossina medicorum* is a carrier of trypanosomes.—*Bull. ent. Res.* **43** pp. 33–42.
- 38 140
- NASH, T. A. M. [1959]. West African Institute for Trypanosomiasis Research. Annual report, 1958.—35 pp.
- NASH, T. A. M. & DAVEY J. T. (1950). The resting habits of *Glossina medicorum*, *G. fusca* and *G. longipalpis*.—*Bull. ent. Res.* **41** pp. 153–157.
- 48 41
- PAGE, W. A. (1959). Some observations on the *fusca* group of tsetse flies (*Glossina*) in the south of Nigeria.—*Bull. ent. Res.* **50** pp. 633–646.



FIG. 1. The habitat of *Glossina medicorum* at Ofankor, showing the thicket, without tall trees, and the short-grass feeding grounds.



FIG. 2. More open grassland with isolated shrubs, towards the top of the hill. Relatively few flies were collected in this area compared with that shown in fig. 1.

DIELDRIN LATTICES APPLIED BY AIRCRAFT FOR
CONTROLLING HOPPERS OF THE RED LOCUST,
NOMADACRIS SEPTEMFASCIATA (SERVILLE).

By W. N. YULE *

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In the past, swarms of adults of the red locust, *Nomadacris septemfasciata* (Serv.), have been formed from dense concentrations of hoppers in its outbreak areas so soon after fledging that control methods employed by the International Red Locust Control Service against the adults have been unable to cope with the peak load of work required in March and April. A two-stage attack on the species was therefore required if emigration of swarms from these areas and the initiation of a widespread locust plague were to be achieved; hopper control would have to be done so that the early peak of adult swarms was prevented, after which control of adults would be carried out over the remainder of the season whenever concentration of adults approached emigration levels. Great advances have been made during the past few years in controlling adult locusts using aircraft (Lloyd, 1959), and, provided hopper control is successful in destroying or scattering concentrations of hoppers so that fledging swarms are few, it has been calculated that two light, spraying aircraft are sufficient to prevent emigration of swarms during the later months. The combination of aerial methods of adult control supplemented by ground methods of hopper control was successful in preventing large-scale swarm emigration for several years. However, the ground methods of hopper control in use during these relatively successful years were expensive, not highly effective, and required a great deal of organisation. Accordingly, when the International Red Locust Control Service (I.R.L.C.S.) purchased its own spraying aircraft in 1956 for the purpose of control of adults, it became desirable to develop an aerial method of hopper control, in order to standardise control methods and to secure round-the-year utilisation of the aircraft. There was hope, too, that an aerial method of hopper control could be found that was cheaper and more effective than existing ground methods of control.

The intensive investigation of an aerial method of hopper control began in the 1957 hopper season, and the work done in that season is described in Lloyd & Yule (1959). Before this, the information available on the newer insecticides had been surveyed. Of the few that were tested in the field, dieldrin was selected as the most suitable for use as a stomach poison, because of its favourable differential toxicity to insects and vertebrates, respectively, persistence, and comparatively low cost (Lloyd, 1955).

The first possibility was direct attack on each hopper band. In a year of heavy infestation the number of bands in the outbreak areas might be of the order of 100,000 (D. L. Gunn, Material for discussion on hopper control policy.—Paper for I.R.L.C.S. council meeting no. TS.56/34/1, 1956), but since the majority of bands tend to be under one acre in size, normal air-to-ground spraying would have required an excessive number of aircraft and ground-marking staff. Aerial spotting for hopper bands without ground assistance was therefore tried,

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but results were not promising (Lloyd & Yule, 1959), and the plan for direct aerial attack on hopper bands was abandoned, although it seemed that aerial searching for large, dense infestations might be useful in a bad year.

The second possibility was that of spraying hopper-infested areas with a persistent stomach poison, in widely spaced strips laid down in two directions at right angles, forming a lattice (lattice-spraying). Hoppers in their migrations might enter these poisoned strips, eat, and die (du Plessis, 1949; Bouriquet, 1954). Preliminary investigations were made of hopper migration and feeding habits, and the effectiveness and persistence of strips treated with dieldrin for poisoning migrating hopper bands was tested (Lloyd & Yule, 1959).

Bands of hoppers were not formed until about the third stage in hopper development. The larger, denser, bands migrated in a fairly constant direction for many days at an average rate of 70 yd. per day, but bandlets moved about at random and their effective displacement from day to day was very small (Yule & Lloyd, 1959). Hoppers in bands apparently fed as they 'marched', and a single swath of dieldrin placed across the path of a migrating band was very effective in destroying them. With this technique, high mortalities were obtained repeatedly by using a single 20-yd. swath containing a dosage of about $4\frac{1}{2}$ oz. dieldrin in $1\frac{1}{4}$ gal. water per acre of swath (= swath-dosage), and the persistence of dieldrin in the field was found to be about 20 days. Studies on migration rates of hopper bands indicated that a square lattice pattern of spraying in which the length of side of the squares was not more than 900 yd. was likely to catch and kill all the hopper bands inside these squares within the three weeks for which the dieldrin persisted. Two operational trials were made of unassisted lattice-spraying of such strips at 300-yd. intervals, and although the unassisted spraying technique resulted in a very irregular lattice pattern, good control seemed to have resulted, as few adults emerged in or near the treated areas (Lloyd & Yule, 1959).

The habitat and life-cycle of the red locust.

The outbreak areas of the red locust are, typically, large open grass plains, which have formed in regions with impeded drainage, and which are normally subject to seasonal flooding and burning (Vesey-FitzGerald, 1955). They occur in the Mweru wa Ntipa in Northern Rhodesia and in the Rukwa Rift Valley and Malagarasi region in western Tanganyika, and their total area is estimated to be about 2,000 sq. miles. By comparison, the invasion areas of the red locust have extended during past plagues over most of Africa south of the equator (Morant, 1947; Gunn, 1952a).

The red locust has only one generation per year in its outbreak areas, and its multiplication potential is reckoned to be about a hundred-fold (Robertson, 1954). The females lay up to three egg-pods after the beginning of the rains, usually starting in mid-November; incubation occupies about four weeks, and the first hoppers are usually seen about mid-December. During growth, the hoppers moult usually six, but sometimes seven times (Burnett, 1951; Albrecht, 1955), and fledging usually begins about the middle of February, but may continue till about the middle of April. The adult locusts remain immature for most of the remainder of the dry season, meantime living and feeding in the grassy habitat of their outbreak areas or else concentrating to form swarms which may emigrate and breed elsewhere. When they become mature they mate, lay eggs, and then die; that is, the cycle usually closes with the calendar year (Faure, 1935).

Materials and methods.

Each of the two I.R.L.C.S. spraying aircraft is a Piper Super-Cub PA-18A, a high-wing monoplane powered by a single 150-h.p. Lycoming engine. Each

is fitted with conventional tank, pump, and boom-and-nozzle spray gear, but can be used for passenger flying on removal of the tank, and installation of a single seat in its place. The insecticide, which for hopper control consists of Dioldrex 15 diluted with various proportions of water to produce an aqueous emulsion, is power-loaded into a 60-gal. (Imperial) tank fitted inside the fuselage and behind the pilot's seat. The liquid flows down into a wind-driven centrifugal pump, which forces it to under-wing booms fitted with spray nozzles (details of the airspray organisation of I.R.L.C.S. are given in Yule, 1959).

The spraying arrangements that have been found to give optimum penetration, coverage, and deposit of dieldrin for lattice treatment are given in Table I.

TABLE I.

The spraying arrangements which have been found to give optimum penetration, coverage, and deposit of dieldrin for control by the lattice method.

(a) Spraying arrangements :					
Type of nozzles	Spraying Systems Teejet 8004 flatspray nozzles
Orientation of nozzles on the spray boom					Pointing vertically downwards
Number of nozzles	About 30, uniformly distributed
Pump pressure..	40 lb./sq. in.
Emission rate	12 gal. per minute
Spraying speed	80 m.p.h.
(b) Results, with dieldrin aqueous emulsion spray at normal field dilutions:					
Drop-spectrum mass-median-diameter (50% volume)	180 microns
Chemical recovery	60%
Volume recovery	30%
Swath width	20 yd., uniform distribution from low-level application
Emitted swath-dosage	4½ ounces dieldrin in 1½ gallons aqueous emulsion spray per acre of swath

To find target areas, the outbreak areas were first line sampled by systematic counts made on foot or using a Land-Rover or a Swamp Skipper (Scheepers & Gunn, 1958). When this preliminary sampling (scouting) revealed an area with a high infestation of hoppers, intensive scouting on foot was used to measure the percentage infestation; this is the percentage of the length of the line samples which passed through infestations of hoppers (Scheepers, Eysell & Gunn, 1958), and is used in this paper as the measure of population size. Samples were taken to determine the proportions of the various hopper instars present, and the boundaries of the infested area were marked with flags. If the infestation was sufficiently large and widespread to warrant lattice treatment for control purposes, each corner of the rectangle that fitted the area most closely was marked with a flag; if the sides were very long (*e.g.*, over 1½ miles), they were marked at intervals of half to one mile with additional flags. Large conspicuous flags of

fluorescent yellow silk material were used and the airmen were able to see them from a long way off. The field officer then informed the pilot and the airfield controller in writing or, when the airfield was inaccessible, orally by V.H.F. radio, of the location and size of the area to be sprayed, any flying hazards that it might contain, the size of lattice to be used, and the concentration of dieldrin solution to be sprayed.

The application of spray in a lattice pattern was done by the pilot without ground assistance, and is termed unassisted lattice-spraying. A method tried in 1957 (Lloyd & Yule, 1959), using rated turns between spray lines to obtain different spacings, was not at all accurate and has been superseded by a method in which the pilot flies first along one edge of the area and then along a second edge, at right angles to the first, dropping swath markers at predetermined intervals of time. Next, starting at one corner, he sprays along a carefully maintained compass course for a predetermined time, using a special compass and stop-watch, over each marker in turn.

Various types of swath markers were tested and rejected, including tale bombs and weighted flags that were intended to come to rest lying flat along the top of the grass. The completely successful marker was found to be a roll of white toilet paper, partly opened and thrown out of the aircraft flying at a height of about 80 ft. above the ground. From this height, the roll did not come undone quite completely and the streamer trailing from the heavy core drifted to lie along the top of the grass, thus forming a conspicuous marker for the airman. When dropped from below 50 ft., too little paper unrolled to form a conspicuous marker, and when dropped from over 100 ft. unrolling was complete before reaching the ground, and the paper drifted far downwind.

The first sortie of a day's control work consisted of surveying the area to be sprayed and distributing markers for the lattice. Sufficient markers for the day's work were dropped during the first sortie, so that all other flying during that day was for spraying. Markers dropped on one day would not serve for the next day's spraying because rain, dew, and wind caused the paper to disintegrate and disappear amongst the long grass. Marking was more accurate when done early in the morning when atmospheric conditions were more stable, and distances and directions were measured more exactly by the pilot. Since it is the ground speed and not the air speed of the aircraft that determines the spacing of markers at timed intervals, the pilot had to estimate the effect of wind by timing over a measured mile in the neighbourhood, before deciding on the time intervals to be used.

For this marking work, unusually painstaking and reliable pilots are required. Moreover, it was found best to fly a special marking sortie, without insecticide, because the airman was then less likely to make mistakes in the marking than he was if the aircraft had a full pay-load. The length of spray run in a set of parallels was determined by timing from one corner flag to the other in the same parallel and along the same direction; all spray-runs in the set were done on a single compass-bearing, and none on the reverse bearing, so that at least some types of error would not affect the regularity of the pattern.

Lattice-spraying is normally done from 6 to 9 a.m. and from 3 to 6 p.m., that is, during the cooler and less windy parts of the day, and spraying altitude is low, from 5 to 10 ft. above ground-level. In this way, losses by thermal convection and by drift are minimised. In order to avoid accidents and inaccuracies due to fatigue, pilots should not in any case fly for spraying for more than six hours per day. During a very intensive campaign, lattice-spraying could presumably be done at all times of the day, but efficiency would be reduced.

All the lattice-spraying that was done for either experimental or actual control purposes during this investigation employed the unassisted layout technique described above, and all of it was done in the North Rukwa outbreak area.

Several ground checks on marker spacings showed that a square lattice with a mesh of as little as 250 yd. could be sprayed rapidly and accurately, with an average error of less than ± 10 per cent. (that is, less than 25 yd. from the correct interval in a 250-yd. lattice). Furthermore, it was found that the individual errors were usually not cumulative, so that although the individual swaths in a lattice might be slightly out of place one way or the other, the specified number of swaths and dosages of dieldrin were actually used in the operational control treatment of the sprayed areas. Using a 250-yd. lattice, an area of about five sq. miles has been sprayed in a 6-hour flying day, and lattices with swaths as much as four miles in length have been sprayed accurately and without difficulty.

The quantitative effects on locust populations over such large areas of a slow-acting poison are not easy to estimate accurately. Daily systematic scouting on foot was done by African assistants for several days before spraying, for assessment of percentage infestation with hoppers (details of the percentage-infestation method of assessing hopper populations are given in Symmons & Carnegie, 1959). After spraying, the size of the surviving hopper population was assessed every second day for four weeks by the same method of scouting on foot, using the same African scouts on the same scouting lines, and the decline in size of the hopper population with time after spraying was recorded (as in fig. 2). On alternate days, mortality was estimated by counting and removing dead and moribund hoppers from within wire sampling rings, each enclosing one sq. yd., which were distributed systematically over the experimental area.

Although the assessment of percentage infestation is not a very satisfactory method of judging and comparing the effects of different control methods, no better method applicable to such large-scale experiments has been suggested. The principal weakness is that the hopper infestations are estimated in yards, with little reference to actual numbers. Since the effects of control are particularly marked in reducing or eliminating dense bands, the percentage mortality is necessarily far higher than the percentage reduction in percentage infestation. Some attempt was therefore made to get over this difficulty by using three grades of density of hoppers, namely *odd* (one here and one there), *scattered* (denser but not close to each other) and *bands*. These are not sharply defined grades, but, with tuition and practice, the scouts came to understand what they meant, and the same men did all the scouting work. It was not possible, however, to relate the densities in the three grades to one another in a quantitative way, so the result of an experiment cannot generally be indicated by a single mortality figure; but, as will be seen, the results are quite clear (fig. 2).

In the 1958 trials, mortality was estimated every second day for four weeks in small plots to measure the persistence of dieldrin. Large-scale sampling to estimate total kills was attempted in the 1959 trials, but was abortive; the highest sampling intensity that could be managed without the system becoming excessively unwieldy for routine checking was 0.25 per cent. (*i.e.*, roughly 12 sq. yd. sampled per acre), which was apparently insufficient to obtain accurate estimates of mortalities (Table III).

Results.

Some information was obtained about band formation in the early instars. In 1959, the trials area (the $7\frac{1}{2}$ -sq.-mile experimental control area where trials 4, 5, 6 & 7 were later done) was scouted about twice weekly, starting soon after hatching began. The percentage infestation by the population (size) and its percentage composition (instar and density grade) in that area on four occasions after hatching, are compared in fig. 1. During the period when only first- and

TABLE II.

Summary of the different conditions and results of the operational trials of dieldrin lattices done in 1958 and 1959.

Trial no.	Date trial begun	Lattice size (yd.)	Swath-dosage dieldrin (oz.)	Area-dosage dieldrin (oz./acre)	Dilution (ratio Dieldrex 15 : water)	Initial percentage infestation	Percentage reduction in 3 weeks			Pre-dominant instar	Persistence of dieldrin (days)	Area (acres)
							Total population	Expected from regression	Hopper bands only			
							Actual					
1	9.ii.58	500	4.5	0.36	1 : 7	6.4	80	74	95	4	26	1120
2	28.ii.58	750	4.5	0.24	1 : 7	5.0	22	24	60	5	22	223
3	28.ii.58	250	4.5	0.72	1 : 7	3.9	75	76	100	5	?	193
4	22.i.59	500	4.5	0.36	1 : 7	2.0	94	98	100	3	> 7	1550
5	22.i.59	500	2.3	0.18	1 : 15	3.15	84	81	100	3	> 9	826
6	22.i.59	750	4.5	0.24	1 : 7	2.0	71	72	100	3	?	1240
7	22.i.59	250	1.1	0.18	1 : 31	3.36	96	98	100	3	> 7	1033

second-instar hoppers were present, the population increased in size as more hoppers hatched, but no bands were recorded. During the third and fourth weeks after the start of hatching, as third-instar hoppers appeared, bands formed and increased in number and size (*cf.* Chapman, 1959; Yule & Lloyd, 1959). Since the percentage infestation apparently went up slightly and certainly did not fall, the implication is that the number of hoppers was rising. Once bands formed, they consisted of all the first three instars. It is not clear how far this formation of bands was due to gregarious behaviour; it was certainly partly due to increase in numbers on the spot (the "virtual concentration" of Kennedy, 1939). If the distribution of hatching in time was representative of all times and places, the results suggest that, since the lattice-spraying is intended primarily to destroy mobile hopper bands, it should not begin much before one month after the first hatching.

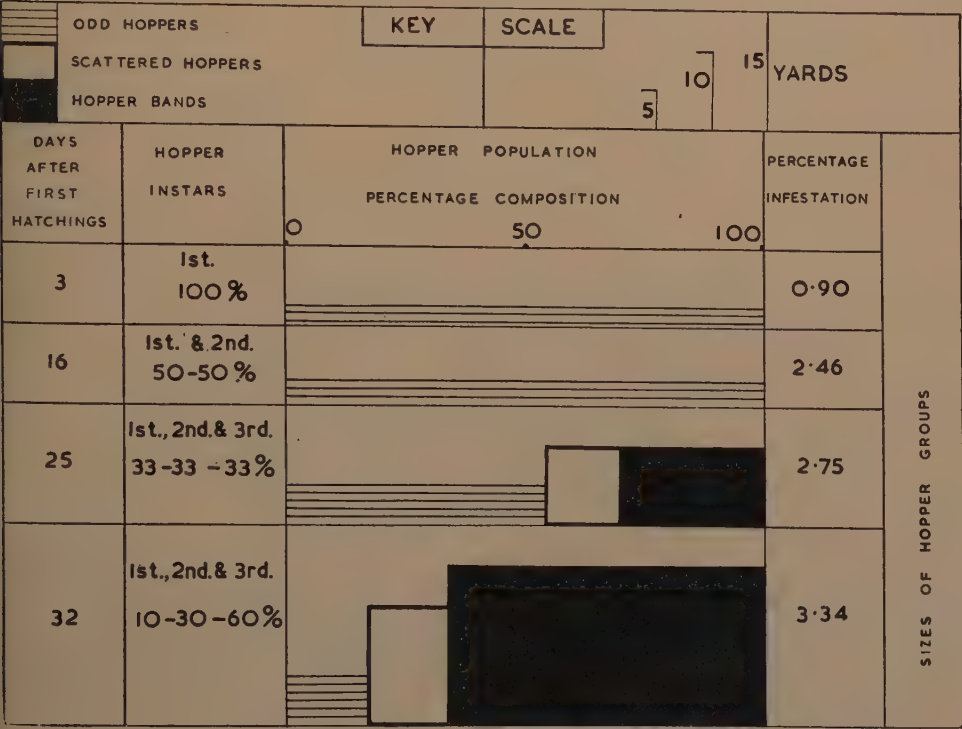


Fig. 1.—Diagrammatic representation of changes which occur in hopper population composition, percentage infestation and group sizes with time after hatching.

The different conditions and results of all the operational trials of dieldrin lattices are summarised in Table II. Trials 1-3 were done in the 1958 hopper season to gain some information on the best lattice-spacing to use. Trials 4-7 were done simultaneously against a single, large, hopper infestation in 1959, using different lattice-spacings and dosages of dieldrin. In this way, the effects of different lattice-spacings and swath-dosages against several hopper populations at various stages of development were tested. Only seven trials could be managed, because each one had to be on a large scale; the time available in each season is short in relation to the four weeks of assessment required, and

TABLE III.
Estimates of the total numbers of hoppers killed with different lattice treatments; 1959 trials.

Trial no. (See Table II)	Mortality estimate : total dead in no. of days (all assessed for 28 days)		Areas of trial plots (acres)	Initial percentage infest- ation of plots with hoppers
	Dead	Days*		
4	31,710,000	7	1,550	2.0
5	6,960,000	9	826	3.15
6	60,000	7	1,240	2.0
7	3,000,000	7	1,033	3.36
Total	41,730,000	—	4,649	—

* No significant mortality occurred after 7 or 9 days.

the assessment requires a large number of trained helpers. Statistical treatment has shown, however, that the data obtained from the trials are remarkably self-consistent. The decline of the initial percentage infestation in trial 5 is illustrated by fig. 2.

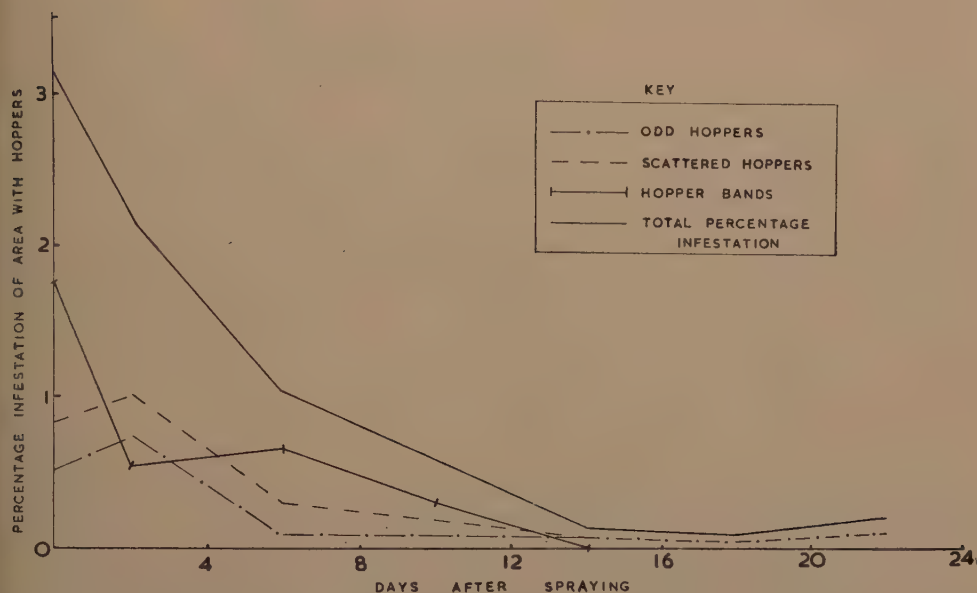


Fig. 2.—Changes in size (percentage infestation) and composition (density grade) of a hopper population with time after treatment with a 500-yd. lattice and swath-dosage of 2.3 oz. dieldrin.

Statistical treatment of results.

A multiple regression was calculated involving the effects of lattice-spacing in yards (\bar{X}_1), swath-dosage in ounces of actual dieldrin emitted per acre of swath in the 20-yard swath (X_2), and hopper instar (X_3), on percentage reduction of the initial infestation size in three weeks (Y) (data from Table II).

The regression equation is:—

$$Y = 187.68 - 0.1041 X_1 + 7.686 X_2 - 24.098 X_3$$

The independent correlations are: highly significant and negative between lattice size and percentage reduction of the initial percentage infestation ($r = -0.852$, $P < 0.01$); probably significant and positive between dieldrin swath-dosage and reduction in population ($r = 0.434$, $0.1 > P > 0.05$); and highly significant and negative between instar and percentage reduction of the initial percentage infestation ($r = -0.915$, $P < 0.01$). The total correlation between percentage reduction of the initial percentage infestation and these three factors is very highly significant ($R = 0.99$, $P < 0.01$).

Using the above equation, it is possible to determine the best time to attack, the dosage of poison and the lattice-spacing which are most effective, and, taking account of the costs of insecticide and of flying, it is possible to choose an appropriate combination of effectiveness and economy.

TABLE IV.

Costs and effectiveness of various combinations of lattice-spacing and swath-dosage of dieldrin on 3rd-, 4th- and 5th-instar hopper populations.

Predominant instar	Lattice size (yd.)	Swath-dosage dieldrin (oz.)	Initial percentage infestation		Cost per sq. mile (sh.)	Most efficient treatments (= A)
			Expected cost of obtaining 1/100th reduction (sh.)	Expected final percentage reduction		
3	250	1.1	2.25	98	482	
	250	2.3	2.76	100	646	
	250	4.5	3.49	100	945	
	500	1.1	1.54	72	241	A.B.
	500	2.3	1.82	81	323	
	500	4.5	2.01	98	473	
	750	1.1	1.61	46	161	
	750	2.3	1.79	55	215	
	750	4.5	2.00	72	315	
4	250	1.1	6.54	74	482	
	250	2.3	7.79	83	646	
	250	4.5	9.47	100	945	
	500	1.1	5.05	48	241	A
	500	2.3	5.67	57	323	
	500	4.5	6.39	74	473	
	750	1.1	7.39	22	161	
	750	2.3	6.97	31	215	
	750	4.5	6.59	48	315	
5	250	1.1	9.72	50	482	
	250	2.3	10.98	59	646	
	250	4.5	12.48	76	945	B
	500	1.1	10.22	24	241	
	500	2.3	9.84	33	323	
	500	4.5	9.50	55	473	
	750	1.1	0	0	161	
	750	2.3	31.70	7	215	
	750	4.5	13.30	24	315	Recommended most useful treatments (=B)

Time of attack.

The third instar is the best stage at which to attack hoppers. It has already been shown (fig. 1) that control by the lattice method against the first and second instars was likely to be ineffective, because few migrating bands were formed before the third instar appeared. In addition, the regression has shown that the effectiveness of a particular treatment decreases as it is applied to instars later than the third (Table IV).

Lattice-spacing and dosage of poison.

The criterion of efficiency used is the cost of reducing the initial percentage infestation by 1/100th over one sq. mile. That cost depends on (a) the flying cost for spraying the given area, which is a function of the lattice-spacing; (b) the cost of the poison at the area-dosage used, which is a function of the swath-dosage and lattice-spacing; and (c) the estimated reduction in percentage infestation achieved by the treatment. The average total cost per flying hour for our aircraft was 269 shillings in 1958, and average time per sortie 35 minutes; the cost per sortie was therefore 157 sh. Dieldrin, landed at Abercorn as Dieldrex 15, cost 1.33 sh. per ounce.

The total cost of treating an area of one sq. mile by the lattice method is therefore:—

$$\text{Total cost} = \frac{2.188 (1.33 \times 11,700 X_2 + 157 \times 242)}{X_1}$$

where the same symbols are used as before.

If this value is divided by Y (from regression equation) the percentage reduction of the initial percentage infestation, we have the cost of reducing the initial percentage infestation by 1/100th with the given treatment. The calculated costs of reducing the initial percentage infestation 1/100th over one sq. mile for the third, fourth and fifth instars, respectively, using three swath-dosages and three lattice-spacings, are given in Table IV. It is again apparent that the third instar is the best time to strike against hoppers. The most efficient combination of lattice-spacing and swath-dosage that can be used is a 500-yd. lattice using a swath-dosage of 1.1 oz. of dieldrin against third-instar hoppers. This treatment would produce a reduction of over 70 per cent. of the initial percentage infestation, at the extremely low total cost of 240 sh. per sq. mile (Table IV).

A criterion of efficiency is the cost per hopper killed, though maximal efficiency in this sense may not be a proper objective (Gunn, 1952b). Very little work has been done on relating percentage infestation of areas with hoppers to total number of hoppers in the area; however, experience, supported by the final results of lattice trials and control operations, strongly suggests that if, say an estimated 75 per cent. reduction in percentage infestation resulted from some treatment, then far more than 75 per cent. of the original number of hoppers have been killed (see p. 445). Nevertheless, if it were the policy to reduce by control all infestations to say 1 per cent., which might be considered a safe surviving infestation, there might be a sufficient number of hoppers remaining in some of the areas which were treated by the most efficient method, to cause trouble by swarming soon after fledging. Thus it might be worthwhile to spend extra money to reduce initially very dangerous hopper infestations by a greater percentage than would be achieved by the most efficient treatment. On the other hand, smaller but still dangerous infestations could be treated by cheaper combinations than the most efficient, where the reduction required to achieve a safe infestation level was less than that resulting from the most efficient treatment. The cheapest way of reducing various initial infestations to various

TABLE V.

The most economical treatments for reducing various initial percentage infestations to a final percentage infestation of 1 or 0.1 per cent. for 3rd-, 4th- and 5th-instar hoppers.

Hopper population	Before treatment	After treatment	Treatment giving nearest result most economically			After treatment
Predominant instar	Initial percentage infestation	Desired final percentage infestation remaining	Lattice-spacing (yd.)	Swath-dosage dieldrin (oz.)	Total cost per sq. mile (sh.)	Actual final percentage infestation remaining
3	10	1	500	4.5	473	0.2
	8	1	500	2.3	323	1.5
	6	1	500	2.3	323	1.08
	4	1	500	1.1	241	1.12
	3	1	500	1.1	241	0.84
	2	1	750	2.3	215	0.90
	1	1	—	—	—	—
	10	0.1	500	4.5	473	0.2
	8	0.1	500	4.5	473	0.2
	6	0.1	500	4.5	473	0.1
	4	0.1	500	4.5	473	0.1
	3	0.1	500	4.5	473	0.1
	2	0.1	500	4.5	473	0
	1	0.1	500	4.5	473	0
4	10	1	250	2.3	646	1.7
	8	1	250	2.3	646	1.4
	6	1	250	2.3	646	1.0
	4	1	500	4.5	473	1.0
	3	1	500	4.5	473	0.8
	2	1	750	4.5	315	0.9
	1	1	—	—	—	—
5	10	1	250	4.5	945	2.4
	8	1	250	4.5	945	1.9
	6	1	250	4.5	945	1.4
	4	1	250	4.5	945	1.0
	3	1	250	2.3	646	1.2
	2	1	500	4.5	473	1.1
	1	1	—	—	—	—

final infestations is shown in Table V. This should act as a guide for control, the method to be used being chosen to suit the initial infestation conditions and the level of control desired.

Mortality estimates for trials 4, 5, 6 and 7 are given in Table III. The low sampling intensity used did not give accurate estimates of total numbers killed, for out of the total of 42 million deaths that were estimated, 32 millions were in trial 4. This trial took place in an area of below average intensity of infestation which covered only about one-third of the whole trials area, yet in which, according to counts of corpses, three-quarters of the total mortality occurred. Estimation of mortality when the area involved is large is known to be of a low order of reliability and has been judged to give an *underestimate* of actual mortalities that occur, for example, because of removal of corpses by scavengers before counting of corpses takes place. Large-scale sampling for mortality was attempted in the 1959 trials for the purpose of checking, or replacing, estimation of decline in population size by the percentage-infestation method of assessment; but, since the results were not self-consistent, no use will be made of the mortality estimates. (The results obtained by the percentage-infestation method of assessment have in any case been estimated to be of a sufficiently high order of reliability for results of different treatments to be compared quite fairly on these data alone, without recourse to mortality figures for support (see p. 445).)

Some operational evidence was obtained to support the experimental findings that the persistence of dieldrin in the field is at least 20 days (Lloyd & Yule, 1959; and Table II).

The decline in percentage infestation with hoppers of an area after lattice treatment, and the effect of the treatment on the various component classes of hopper groups, is shown in fig. 2. The effects which are illustrated in fig. 2 are from trial 5, and are typical of a 500-yd. lattice; a 250-yd. lattice shows a similar effect in a much shorter time, and the effect of a 750-yd. lattice seems to be inconsistent and is slower than that of the 500-yd. lattice. It can be seen from fig. 2 that a 500-yd. lattice treatment caused a decline in size of a hopper population mainly through destruction of hopper bands, which in this case were all eliminated inside two weeks after spraying. A large proportion of odd and scattered hoppers must also have been killed, however, since the final percentage reduction in infestation size in this case was 84 per cent. and bands constituted only 56 per cent. of the initial infested area.

Discussion.

Effectiveness of the lattice method of control.

Statistical treatment of the results has shown that, as might be expected, the effectiveness of control decreases with increasing instar (age of hopper) (*cf.* Gunn, Lloyd & Davey, 1954), decreases with increasing lattice-spacing, and increases with increasing swath-dosage of dieldrin. The multiple-regression analysis has also shown that these three factors determine the reduction in percentage infestation almost completely, and the results of various combinations of treatment may be calculated accurately. From the calculated results of several combinations of treatment given in Table IV, it is evident that even a wide lattice-spacing or low swath-dosage of poison gives a useful kill against instars 3 and 4, but a closer lattice and increased swath-dosage are required to obtain satisfactory results against instar 5. Using 50 per cent. control as the lowest margin of effectiveness that is useful, it can be seen from Table IV that by varying the control treatments used against any one instar or against different instars, various levels of control in the range 50–100 per cent. can be obtained as desired.

Introducing cost as another factor, and considering cost per unit percentage

reduction in population size as a measure of efficiency, the efficiency of various treatments and the total cost and effectiveness of each of these treatments applied over one square mile of infested area has been calculated (Table IV). The most efficient treatment can therefore be chosen for use against each instar (A in Table IV), or various levels of control may be obtained at different costs against any one instar or against different instars, by choosing the appropriate treatment to use. If policy and current infestation conditions dictated that all hopper populations had to be reduced to a safe level of 1 or 0.1 per cent. infestation, the best treatments for use against different initial infestations to achieve the safe surviving infestation decreed could be calculated (*e.g.*, Table V). Calculations of this sort could form the basis for organising the most efficient hopper control campaign that is possible with the dieldrin-lattice method of control.

Up to now, hopper control has been aimed at reducing infestations so that the main attack, which is aerial control of adults, could be spread out to prevent swarm emigration by effectively destroying concentrations of adults as they occurred throughout the season of adult diapause. Even this limited objective has been very difficult to achieve in the past, however, because no highly effective method of hopper control was available. Various mechanised and manual methods of controlling hoppers, using BHC dust and spray were tried; the manual methods proved to be more practical under the swampy conditions prevailing in the outbreak areas during the hopper season, and a fairly effective manual method for the application of BHC known as "puffer-dusting" was eventually developed (Lloyd, 1959). We have now developed an aerial method of hopper control which seems to be both effective and economical, and allows us to standardise control methods and obtain better utilisation for our spray aircraft. We should, therefore, first compare it with the previous method of BHC hand puffer-dusting in terms of relative effectiveness, economy, and practicability, to ascertain whether any improvements have been made in our ability to control hoppers.

Comparison of the puffer-dusting and dieldrin-lattice methods of hopper control.

To control hoppers by BHC puffer-dusting, teams of African labourers combed the plains and puffer-dusted any concentrations of hoppers they found. About 1,000 Africans had to be employed as casual labourers every hopper season, and it has been calculated that four acres could be searched and controlled per man-day, at an average cost of 4.5 sh. per acre searched and controlled (Lloyd, 1959). About 50 per cent. control over whole areas was the result generally achieved (D. L. Gunn, Changes in insecticide-control policy.—Paper for I.R.L.C.S. council meeting no TS.57/36/1, 1957). From these data, and considering hopper development to cover 64 days (Faure, 1935), it can be calculated that 50 per cent. hopper control could be obtained over an area of 400 sq. miles at a total direct cost (insecticide & labour) of 1,160,000 sh. (£58,000). In practice, however, the maximum expenditure on hopper control by ground methods that has ever occurred was in 1955, when a sum of £28,000 was spent on hopper control, and the situation had still to be saved by aircraft attack on adults in March (Gunn, *loc. cit.*, 1956). The potential scale of attack for puffer-dusting given above (400 sq. miles) is therefore about twice the actual scale that has been achieved at maximum effort.

No large-scale hopper control campaign using aerially-applied dieldrin lattices has occurred so far, but some experience of the capacity of the method has been obtained. An area of 5 sq. miles has been lattice-sprayed in one six-hour flying day using a 250-yd. lattice (see p. 445). If instars 3, 4 and 5 only were attacked (= 30 days. Faure, 1935), using 500-yd. lattices against instars 3 and 4 and swath-dosages of 1.1 and 4.5 oz. dieldrin per acre, respectively, and a 250-yd. lattice and swath-dosage of 4.5 oz. dieldrin per acre against instar 5 (B in Table IV), then if we obtained 66 per cent. aircraft serviceability, an area of

330 sq. miles could be treated during the duration of instars 3, 4 and 5 by our two spray aircraft. The total direct cost of these treatments (insecticide and aircraft) would be about £10,000, and a minimum of 75 per cent. control should be obtained (Table IV). Extrapolating from the results, it can be calculated from the regression that about 60 per cent. control over an area of 36 sq. miles might be achieved against sixth-instar hoppers using a 150-yd. lattice and swath-dosage of 4.5 oz. dieldrin per acre, but at the very high cost of about £80 per sq. mile. It would be relatively uneconomical, therefore, to attack sixth-instar hoppers with dieldrin lattices, and attack should be concentrated against instars 3, 4 and 5 for best results.

Much of the above calculation of performance and costs of the two methods involves a good deal of theorising; for example, no single-instar populations of red locust hoppers ever occur (Smee, 1936), and rates of development vary (Faure, 1935; Burnett, 1951; Albrecht, 1955), but the basic facts are sound (Lloyd, 1959; and Table IV), and the comparison should be indicative of the actual state of affairs.

Scale of attack.—Preliminary sampling of the outbreak areas for location of infested areas is required in both methods. Modern methods of scouting using Land-Rover and Swamp Skipper (Scheepers & Gunn, 1958) are superior in terms of potential scale of searching than the old method of scouting on foot. Application of dieldrin lattices against all dangerous hopper infestations occurring in the outbreak areas, or in a bad season against only the more severe infestations, should therefore be possible. Furthermore, recent research on the operational value of protecting the outbreak areas from fire has shown that specially burnt areas to act as egg-laying traps are effective in localising breeding (P. M. Symmons, unpublished report, I.R.L.C.S., 1959), so that the scale of attack required against hoppers may become smaller as protection from fire is developed and extended.

From the calculations of the potential scales of attack of the two methods of hopper control given above, it appears that with the dieldrin-lattice method, although economically applicable only against instars 3, 4 and 5, control could be effected over an area of 330 sq. miles of hopper infestations, whereas puffer-dusting against all the hopper instars, at maximum effort, has in the past achieved control over only about 200 sq. miles of hopper infestations.

Effectiveness.—The control level generally achieved over whole areas with BHC hand puffer-dusting was 50 per cent. and costs rose and effectiveness declined with increasing infestation (Gunn, *loc. cit.*, 1957). The lattice treatments given in the above calculations (B in Table IV) would give about 75 per cent. reduction in percentage infestation over a whole area, which is thought to indicate a much higher percentage mortality, so that the dieldrin-lattice method of hopper control is more effective and more flexible than puffer-dusting (Table IV). Moreover, the effect of the *same* lattice treatment should increase with increasing infestation, as there are likely to be more hopper bands in a denser infestation (Scheepers, Eyssell & Gunn, 1958).

Cost.—The costs of the various lattice treatments that would be economical for a certain degree of effectiveness against different instars vary considerably. The most efficient treatment of all is the 500-yd. lattice and dosage of 1.1 oz. per acre of swath against the third instar (Table IV). This treatment would give a minimum of 72 per cent. control over one sq. mile at a total direct cost of 240 sh., that is, at 0.375 sh. per acre, but to obtain the same level of control of a sq. mile infestation of fifth-instar hoppers would cost about 940 sh., that is, about 1.5 sh. per acre (Table IV). A fair average cost for lattice treatment of one sq. mile of *any level* of infestation of third-, fourth- or fifth-instar hoppers to give a minimum of 75 per cent. control would be about 640 sh., that is, 1.0 sh. per acre (Table IV). In comparison, the average performance and costs of puffer-dusting

indicate that 50 per cent. control of one sq. mile of infested area could be obtained at a cost of 2,880 sh., or 4.5 sh. per acre (Lloyd, 1959). This cost would become smaller when a low infestation was being attacked, and would increase as infestation intensity increased. Only where very small infestations of hoppers were attacked would puffer-dusting approach lattice treatment in terms of economy, and in most circumstances of infestation requiring control, lattice treatment for hopper control would be many times more economical than puffer-dusting.

Organisation required.—One of the limiting factors with the puffer-dusting method of hopper control was the supply of casual labour. Obviously, a locust-control method that has such great dependence on a seasonal supply of large numbers of casual labourers is undesirable. Besides this, the organisation required for recruiting, housing, feeding and supervising a large labour force was considerable, and the administrative and mechanical costs involved absorbed a large portion of the resources of the Service. On the other hand, a small number of European officers and African scouts, for finding and marking hopper infestations, are sufficient ground staff in the field for control by the lattice method. Thereafter, the pilots do the actual control operations without ground assistance, and only the airfield controller and a few labourers for mixing and loading insecticide are required in addition. Aircraft which have to be on hand for adult control later in the year are utilised in control of hoppers by the lattice method, and considering the economies that can be made in staff, organisation, transport and insecticide, the expenditure involved both directly and indirectly in the lattice method is much less than that involved with the puffer-dusting control method.

Recommendations.

To summarise, an aerial method of hopper control has been developed which is more effective and cheaper than the best previous ground method of hopper control; its large-scale operational practicability is also much superior. If ground methods of hopper control have been sufficiently effective in previous years for reducing the pressure of early-season demand for control of adults using aircraft, then it is obvious that with the dieldrin-lattice method of hopper control, we should be able to do at least as much with greater economy and security. Furthermore, such are the potentialities of this new aerial method of hopper control (effectiveness, scope, cost), that it might now be worth while to change the strategy of control to concentrate more on attacking hoppers, thus reducing the amount of relatively more risky and more expensive control of adults that has to be done in any one year. The control operations carried out against hoppers in one of the outbreak areas in the 1959 season, described below, might serve to illustrate the possible advantages of concentrating attack against hoppers rather than adults. Not enough is known about natural mortality to bring it into this initial comparison.

Hopper control in the North Rukwa outbreak area was done entirely using unassisted dieldrin-lattice treatment. In January, during the second instar, the whole area was systematically scouted using the Swamp Skipper and Land-Rover line-sampling method referred to above, and the areas infested with hoppers were mapped. Hopper control was started during the third instar by lattice treatment of these infested areas, and altogether 44 sq. miles were treated, mostly with 250-yd. lattices (for safety's sake, as the lattice-control method was still in the operational experimental stage). Only three Europeans (one pilot, one airfield controller, and one field scouting and marking officer), assisted by about six Africans, were engaged directly in the North Rukwa hopper campaign, and only a small part of their time was spent continuously on the control operations. Altogether, 483 gallons of Dieldrex 15 in 4,258 gallons of water were sprayed in lattice form over an area of 44 sq. miles by one aircraft in 43 flying hours,

and the total direct cost of these operations was about £1,500. If no hopper control had been done in North Rukwa, it has been estimated that an adult population of at least 60 millions would have fledged. This estimate was made from the numbers of adults which actually fledged from an experimental plot which was deliberately left untreated and which contained about 9 per cent. of the total infested area. Only 6.5 million adult locusts did fledge outside the experimental plot (where a further 5 millions fledged), so that, if we assume that a total of 60 million adults could have fledged, then 89 per cent. of the potential adult population outside the experimental plot was destroyed by hopper control. In fact, the percentage killed was probably higher still (P. M. Symmons, unpublished report, I.R.L.C.S., 1959).

Although the above conditions of infestation were not typical of a serious upsurge, the fact that a reduction of 89 per cent. in the population of hoppers that hatched was achieved by a proportionately small-scale hopper campaign using dieldrin lattices is probably indicative of the potentialities of the new method of hopper control. A much greater area could have been treated with ease, and in future control operations against hoppers the most efficient lattice treatments for the particular conditions of infestation in each area requiring control will be used, thus obtaining the same degree of control at lower cost. Also, it was found that approximately 97 per cent. of the population of hoppers that hatched was associated with burnt ground. Accordingly, if the infestation had been very much larger than it actually was, there is no reason to believe that the area infested would have increased to any great extent, so that the *same* lattice treatments of the *same* infested areas as above would probably still have reduced the population of hoppers that hatched by about 90 per cent., perhaps even more, as the infestations would be denser.

In 1954, an upsurge of the red locust occurred in the North Rukwa outbreak area. Intensive control of both hoppers and adults achieved an estimated final reduction of 93 per cent. of the population that hatched. About 49 per cent. reduction in population was achieved during hopper control by ground methods, and the remaining 44 per cent. kill was achieved by ground and aerial spraying of adults. Again, in 1955, very successful breeding necessitated widespread control operations in most of the outbreak areas. In North Rukwa, of the total percentage reduction in population obtained by control, about 22 per cent. was achieved by hopper control, and 78 per cent. by attack on the adults (Lloyd, 1959). Two or three small swarms escaped completely during these bad years (both in 1954), and there would have been many more escapes but for the extensive use of light, spraying aircraft against adults; but these relatively successful campaigns were very costly.

Control of adults by aerial application of 20 per cent. DNC (dinitro-ortho-cresol) oil solution over dense concentrations of locusts costs about 16 sh. per acre (Lloyd, 1959). Control of hoppers by the lattice method costs an average of about 1.0 sh. per acre. Too little is yet known about numbers and densities of hoppers to be able to compare costs per locust killed as hopper and adult. However, if 90 per cent. control of a population hatched in a *whole outbreak area* can be obtained at a cost of about £1,500 using the new lattice method of hopper control (see above), it is fairly obvious that such an over-all level of control, by attack on the adults, would be very much more expensive when there were many locusts, if it could be achieved, and much less effective when there were few.

It would seem reasonable, therefore, to suggest that a reversal of the rôles of control of hoppers and adults be considered. That is, instead of control of hoppers being only a supplement to control of adults, it should now, using the new lattice method of control, become the primary strategy in control. Such a strategy should bring considerable direct economies and increased security, as adult control would be required only to safeguard against small-scale swarm

emigration. The lattice method of controlling hoppers has not yet been tested in a bad year, however, so that it is still to some degree unproven as a reliable control method. It is suggested, therefore, that in order to test the recommended new strategy, full-scale attack on hoppers should be made at the earliest opportunity, and the numbers of adults arising from hoppers surviving this control and the amount and cost of subsequent control of adults required, should be assessed carefully. This would involve little additional risk even in a bad year, as the full potential for control of adults would still be available to deal with any dangerous situation that might arise.

In conclusion, we may say that with such efficient methods of control with chemicals as we have today, aided and supported by advances in scouting (Scheepers & Gunn, 1958), forecasting of populations (Symmons, 1959), and protection from fire (Symmons & Carnegie, 1959), the occurrence of a plague of the red locust in Africa, originating from the known outbreak areas controlled by the International Red Locust Control Service, should be an event of the past.

Summary.

Large-scale operational trials of dieldrin lattices applied by aircraft for controlling hoppers of the red locust, *Nomadacris septemfasciata* (Serv.), were carried out in the North Rukwa outbreak area in south-western Tanganyika during 1958 and 1959. Single swaths of dieldrin aqueous emulsion spray were applied by aircraft to vegetation at wide intervals and in two directions at 90°, forming a rectilinear lattice distribution of poisoned strips of vegetation over large, hopper-infested areas. Hoppers, especially those in bands, were killed on eating the poisoned vegetation in the strips which they encountered during their migrations. An accurate method of lattice layout by aircraft pilots without assistance from ground marking parties was developed, and the whole operation was used on a large scale for controlling the hopper infestation in North Rukwa in 1959.

The results of seven trials, using several lattice-spacings and dosages of dieldrin against different instars of hoppers, indicated that various useful levels of control could be obtained with different combinations of these three factors. Combinations of lattice-spacings of from 250 to 750 yd. with dieldrin swath-dosages of from 1.1 to 4.5 oz. per acre of swath against the third, fourth and fifth instars were calculated to give 50–100 per cent. control of various infestation levels of these three instars, at a cost of from 0.375 to 1.5 sh. per acre. It was calculated that a total infested area of 330 sq. miles could be sprayed with lattices by two aircraft in the duration of the third, fourth and fifth instars.

The aerial dieldrin-lattice method is compared with the best previous ground method of hopper control, and it is shown that the new method is cheaper, more effective, and more practicable than the old method, besides enabling fuller aircraft utilisation and further simplification of organisation to be obtained. A change in control strategy to concentrate once more on hoppers rather than adult locusts, as in the recent past, is recommended, so that preventive control of the red locust could be obtained with greater economy and security.

Acknowledgements.

I have to thank many members of the staff of I.R.L.C.S. for their willing assistance, advice, and criticism during all phases of this work. In particular, Mr. P. M. Symmons has earned my gratitude for undertaking the statistical treatment of the experimental results, and for helping with the preparation of this account for publication. Mr. T. Malujlo, staff pilot, has helped considerably with the development of the unassisted aerial lattice-spraying method, and his

enthusiasm and skill are to be highly commended. Finally, my most grateful thanks are due to Dr. D. L. Gunn, Director of I.R.L.C.S., for his continued help and encouragement throughout the work.

References.

- ALBRECHT, F. O. (1955). La densité des populations et la croissance chez *Schistocerca gregaria* (Forsk.) et *Nomadacris septemfasciata* (Serv.); la mue d'ajustement.—*J. Agric. trop. Bot. appl.* **2** pp. 109–192.
- BOURIQUET, G. (1954). La lutte antiacridienne dans les territoires français d'outre-mer.—*Proc. 6th Symp. Colston Res. Soc., Bristol 1953* pp. 35–39.
- BURNETT, G. F. (1951). Observations on the life-history of the red locust, *Nomadacris septemfasciata* (Serv.) in the solitary phase.—*Bull. ent. Res.* **42** pp. 473–490.
- CHAPMAN, R. F. (1959). Field observations on the behaviour of hoppers of the red locust (*Nomadacris septemfasciata* Serville).—*Anti-Locust Bull.* no. 33, 51 pp.
- FAURE, J. C. (1935). The life history of the red locust (*Nomadacris septemfasciata* (Serville)).—*Bull. Dep. Agric. S. Afr.* no. 144, 32 pp.
- GUNN, D. L. (1952a). The red locust.—*J. R. Soc. Arts* **100** pp. 261–284.
- GUNN, D. L. (1952b). Control of red locusts by insecticides.—*J. Sci. Fd Agric.* **3** pp. 289–296.
- GUNN, D. L., LLOYD, J. H. & DAVEY, P. M. (1954). The choice of insecticides for destroying red locusts in their outbreak areas.—*J. ent. Soc. S. Afr.* **17** pp. 246–251.
- KENNEDY, J. S. (1939). The behaviour of the desert locust (*Schistocerca gregaria* (Forsk.)) (Orthopt.) in an outbreak centre.—*Trans. R. ent. Soc. Lond.* **89** pp. 385–542.
- LLOYD, J. H. (1955). Research (c).—*Rep. int. Red Locust Contr. Serv. 1954* pp. 33–39.
- LLOYD, J. H. (1959). Operational research on preventive control of the red locust (*Nomadacris septemfasciata* Serville) by insecticides.—*Anti-Locust Bull.* no. 35, 65 pp.
- LLOYD, J. H. & YULE, W. N. (1959). Investigations on the use of light spraying aircraft against hoppers.—*Anti-Locust Bull.* no. 35 pp. 24–35.
- MORANT, V. (1947). Migrations and breeding of the red locust (*Nomadacris septemfasciata* Serville) in Africa, 1927–1945.—*Anti-Locust Mem.* no. 2, 60 pp.
- DU PLESSIS, C. (1949). Recent advances in the control of locusts in South Africa.—*J. ent. Soc. S. Afr.* **12** pp. 3–12.
- ROBERTSON, I. A. D. (1954). The numbers of eggs in pods of the red locust, *Nomadacris septemfasciata* (Serville) (Orth., Acrididae).—*Ent. mon. Mag.* **90** pp. 254–255.
- SCHEEPERS, C. C., EYSEL, B. J. & GUNN, D. L. (1958). Density distributions of hoppers of the red locust, *Nomadacris septemfasciata* (Serv.) (Orth., Acrid.), in relation to control by insecticides.—*Bull. ent. Res.* **49** pp. 467–478.

- SCHEEPERS, C. C. & GUNN, D. L. (1958). Enumerating populations of adults of the red locust, *Nomadacris septemfasciata* (Serville), in its outbreak areas in East and Central Africa.—*Bull. ent. Res.* **49** pp. 273–285.
- SMEE, C. (1936). Notes on the red locust (*Nomadacris septemfasciata*, Serv.) in Nyasaland 1933–34.—*Bull. ent. Res.* **27** pp. 15–35.
- SYMMONS, P. (1959). The effect of climate and weather on the numbers of the red locust, *Nomadacris septemfasciata* (Serv.), in the Rukwa Valley outbreak area.—*Bull. ent. Res.* **50** pp. 507–521.
- SYMMONS, P. & CARNEGIE, A. J. M. (1959). Some factors affecting breeding and oviposition of the red locust, *Nomadacris septemfasciata* (Serv.).—*Bull. ent. Res.* **50** pp. 333–353.
- VESEY-FITZGERALD, D. F. (1955). The vegetation of the outbreak areas of the red locust (*Nomadacris septemfasciata* Serv.) in Tanganyika and Northern Rhodesia.—*Anti-Locust Bull.* no. 20, 31 pp.
- YULE, W. N. (1959). The eighth plague.—*Shell Aviat. News* no. 253 pp. 15–19.
- YULE, W. N. & LLOYD, J. H. (1959). Observations on migration of hopper bands of the red locust (*Nomadacris septemfasciata* Serville) in an outbreak area.—*J. ent. Soc. S. Afr.* **22** pp. 233–244.

THE FLIGHT OF *CULICOIDES IMPUNCTATUS* GOETGHEBUER
(DIPTERA, CERATOPOGONIDAE) OVER MOORLAND AND
ITS BEARING ON MIDGE CONTROL.

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(PLATE XIII.)

For some time now it has been increasingly difficult to reconcile all the available data bearing on the control of *Culicoides impunctatus* Goetgh. in Scotland. On the one hand, there have been highly satisfactory larvicidal trials on Soutra Hill, Midlothian (Kettle, Nash & Hopkins, 1956; Kettle & Parish, 1957; Kettle, Parish & Parish, 1959), and on the other the failures of the full-scale field trial at Loch Maree, Wester Ross (Parish & Kettle, 1957) and of the hotel pilot scheme (Parish, 1958). In the latter, observations were scattered throughout Scotland from Carsphairn in the south to Seourie in the north, so that the failure could not be attributed to local conditions.

In the larvicidal trials, insecticides were applied to small plots and the degree of control assessed by sampling the larval population. In these experiments it was found that there was considerable delay between the application of insecticide and attainment of full control. This delay was associated with the need for a large amount of rain (over 20 in.) to wash the insecticide down through the layer of living moss to the peat in which the larvae live. Once this initial period had passed, a high degree of larval control was attained, which remained effective for at least three years. However, from the practical point of view, the important feature is the number of adult midges biting, not the presence or absence of larvae in the soil, and in this connection the results of sampling for larval mortality due to insecticide treatment are unimportant, except in so far as they indicate the size of the adult population to follow. Consequently, in the subsequent full-scale field trials the degree of control was based on adult catches. It would have been ideal to have based this assessment on both adult and larval populations but the time- and labour-consuming nature of larval sampling rendered this impractical, and a choice had to be made between the two. Since it is the adults that cause the nuisance, the estimation had to be based on adult populations, but the absence of larval data was a great handicap in interpreting the results obtained.

The first full-scale trial took place at Loch Maree. Treatment was applied in May and June 1955, and was followed by an abnormally prolonged spell of hot, dry weather during which the insecticide remained as a thin film on the vegetation exposed to insolation. There was adequate rain during the winter of 1955-56 to wash the insecticide into the soil, but the results in the summer of 1956 were disappointing. The estimated reduction in numbers of adults was only about 25 per cent. With the data available it was not possible to differentiate between a failure of the insecticidal treatment and an error in the argument on which the trial was based. At that time one was inclined to attribute it to the abnormal weather, because it is known that thin films of DDT can be rendered insecticidally inactive by exposure to sunlight (Metcalf, 1955).

Before this result was available, the hotel sites were sprayed in the spring of 1956. The summer which followed was very wet and there was no question

of inactivation of the insecticide by sunlight. Yet when, at the end of 1957, the results for these sites became available, it was clear that the control attained fell far short of that desired. In fact, when the data from all the sites were amalgamated, the control achieved was again about 25 per cent.

With these two failures in mind it became necessary to examine the basis of the control technique. The factor which links together larval control and adult abundance is the flight range of the species. In this case it had been argued, on the evidence of field observations by Kettle (1951) near Glasgow, that the density (per cent. survival) of females of *C. impunctatus* would fall to 1/10th with every 65 yd. distance from the breeding site, and hence at 200 yd. the adult density would be about 1/1,000th of the original value (fig. 1). From this it has been argued that if all the breeding sites within 200 yd. of a location were made unproductive of *C. impunctatus* by some means such as insecticidal treatment then that place should be rendered free from midges.

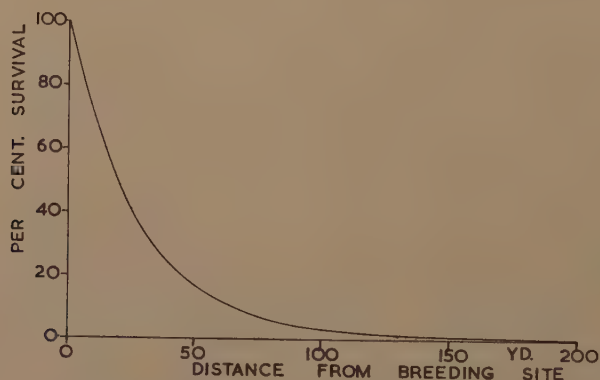


Fig. 1.—Density/distance regression of females of *C. impunctatus* through woodland (data from Kettle, 1951).

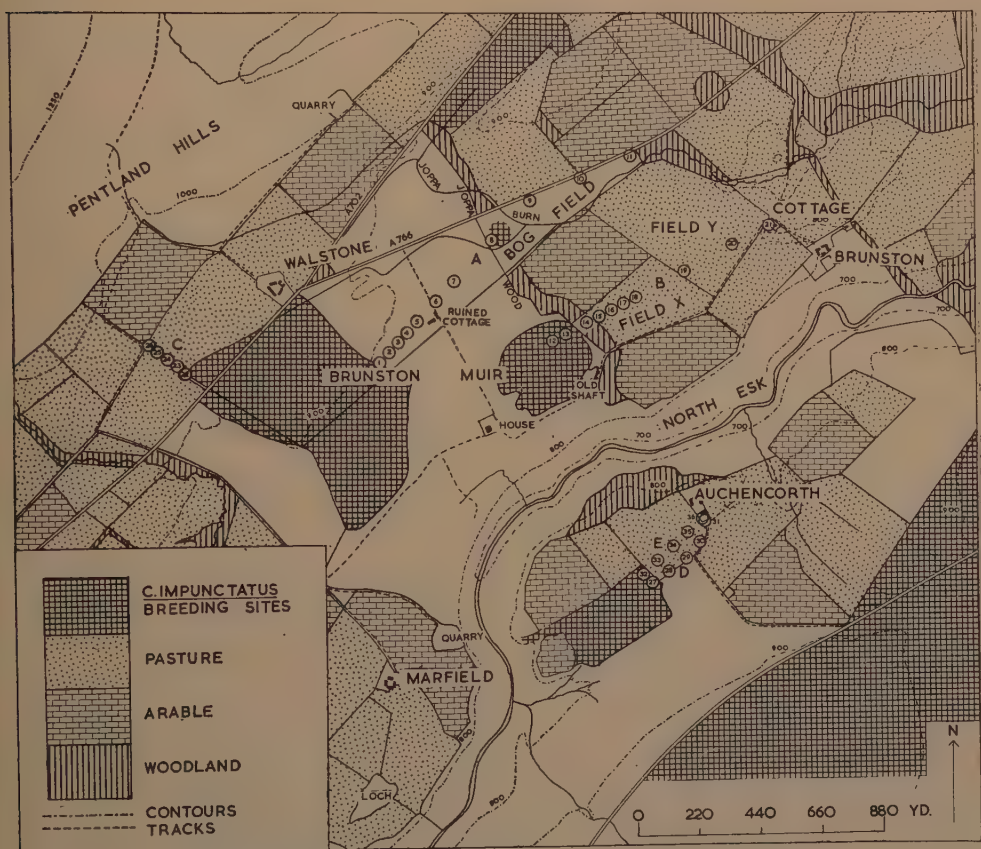
These original flight-range observations of Kettle were made, as stated clearly in the title of the paper, through woodland. It may well be that, in the open, midges might be carried considerably further than 200 yd. by the wind. Observations by Miss Rachel Reuben (unpublished information) indicate that *C. impunctatus* is active when the air speed is 3 m.p.h. or less. Even at 1 m.p.h. a midge would only have to be carried passively by the wind for less than 10 minutes to go more than 200 yd.

It therefore became imperative to obtain further data on the flight range of *C. impunctatus*, especially in the direction of the prevailing wind. To this end, trapping experiments were conducted in the vicinity of Brunston Muir, eleven miles south-west of Edinburgh.

Ideally one would have liked to have found an isolated circular breeding site from which dispersion could be measured in all directions, or alternatively a breeding site with a straight, clear-cut edge at right angles to the prevailing wind. Such ideal conditions are very difficult to find, and it was necessary to accept an alternative where the area of breeding could be defined by inspection and to measure dispersal from it. It has already been shown (Kettle & Lawson, 1952, Table IV, p. 250) that breeding of *C. impunctatus* is largely (99%) restricted to bogland, i.e., wet, organic soil bearing *Sphagnum* spp. and *Polytrichum commune*, so that breeding sites of *C. impunctatus* and bogland can be regarded as co-extensive.

Topography of Brunston Muir and arrangement of experiments.

Brunston Muir lies to the east of the Pentland Hills (fig. 2) and south of A 766 near its junction with the main Edinburgh-Biggar road A 702, at an elevation of 900 ft. above sea-level. The countryside around is intensively farmed. The Muir is roughly diamond shaped with the sides facing NE., SE., SW. and NW. The north-eastern side is separated by a boundary wall from a narrow



BRUNSTON MUIR ENVIRONS

Fig. 2.—Brunston Muir and its environs. Open, numbered circles indicate trap positions and numbers. Unshaded area represents hill and moorland grazing.

strip of woodland (Joppa Wood) which will act as a wind-break to the prevailing south-westerly winds. The south-eastern side is formed by the river North Esk, which here flows at the bottom of a gorge more than 100 ft. deep. On the south side of the river there is Auchencorth farm, which is surrounded by grassy fields except for an isolated patch of bogland to the south-west. The south-west side adjoins the arable fields of Marfield farm. To the north-west the Muir is limited by the roads except for a patch of bogland north of the road in the field adjoining Walstone farm. This patch has a well-defined straight edge which runs roughly in a south-west-north-east direction.

TABLE I.

Notes on the domestic stock present in the same fields as the various traps.

Line & trap nos.										
	A 1-7	A 8-11	B 12 & 13	B 14-18	B 19 & 20	B 21 (in cot- tage garden)	C 22-26	D 27 E 32	D 28-30 E 33-35	D 31 E 36 (in farm garden)
27 May	sheep	nil	sheep	nil	milking cattle	nil	sheep & cattle	sheep	horse, rams, cow	nil
2 June	sheep	nil	sheep	heifers & bullocks	milking cattle	nil	sheep & cattle	sheep	horse, rams	nil
9 June	sheep	nil	sheep	heifers & bullocks	milking cattle	nil	sheep & cattle	sheep	horse, rams, cattle	nil
16 June	sheep	nil	sheep	nil	milking cattle	nil	sheep & cattle	sheep	horse, rams	nil
23 June	sheep	nil	sheep	nil	milking cattle	nil	sheep & cattle	sheep	horse, rams	nil
30 June	sheep	nil	sheep	nil	milking cattle	nil	sheep & cattle	sheep	horse, rams, cows	nil
4 July	sheep	nil	sheep	nil	milking cattle	nil	sheep & cattle	sheep	horse, rams, heifers	nil
7 July	sheep	young calves	sheep	nil	milking cattle	nil	sheep & cattle	sheep	horse, heifers	nil

In this area the prevailing wind is west to south-west and therefore little attention was paid to the south-west corner as the interest centred on the maximum flight range and not on flight against the wind.

In order to keep the work within reasonable limits it was decided to restrict the observation to thirty-six traps which were to be changed weekly. The layout presented much difficulty and the final arrangement was by no means free from criticism. Five separate lines of traps were erected, of which three were short and two long.

In view of the previous observations of Kettle (1951), considerable emphasis was placed on the first 200 yd. from the breeding site. Therefore traps were erected at 0, 50, 100, 150 and 200 yd. in all lines and the short lines only contained these five traps.

One short one (C) took advantage of the clearly defined edge to the bogland near Walstone, to determine flight at right angles to the prevailing wind. This line of traps ran close to a fence dividing two pasture fields in which cattle and sheep grazed throughout the whole of the experiment (Table I). In the middle of the fence (80 yd. from the bog) there was a gate which was permanently open so that animals passed freely from field to field.

The other two short lines were sited at Auchencorth farm, south of the North Esk river. Here, flight was measured between the nearby bogland and the inhabited farmhouse about 250 yd. away. In many respects this site can be compared to one of the hotel trials. In both cases there was an inhabited building as the focal point of interest. In the hotel experiments, midge breeding was eliminated from the nearby ground, *i.e.*, within 200 yd. of the hotel, with insecticides while at Auchencorth farm there was no nearby midge breeding to eliminate, the nearest site being 250 yd. away. This experiment would indicate whether the absence of breeding for 250 yd. around an inhabited building would be adequate to protect it from invasion by *C. impunctatus*. It is equivalent to a hotel experiment in which the insecticidal treatment has been completely successful.

The breeding site was most favourably placed for invading the farm as the prevailing winds blew from it to the farm across a well-drained grassy pasture field. There was one wet patch where the field adjoined the bogland and this was the probable source of *C. pulicaris* (L.) trapped in this area. The field contained a flock of yearling rams and a horse for the whole length of the experiment and periodically varying numbers of dairy cattle were pastured there. (See Table I—lines D and E.)

It was hoped to put the traps in a straight line across the field from the bog to the farm. However, Mr. Stoddart, the farmer, pointed out that the horse would almost certainly knock them over unless they were erected against the surrounding wall. In any event, two lines (D and E) were erected, of which one trap in each line was on the bog and one in the farm's front garden. The other three traps in one line (D) were arranged close to the wall and in the other (E) went straight across the field. In spite of the farmer's co-operation in re-erecting the traps as they were knocked down, the horse won and no worthwhile results were obtained from this line (E).

The use of Brunston Muir as a source of *C. impunctatus* was complicated by the existence of Joppa Wood to leeward, as it was desired to measure flight range over open moorland. It was conceivable that *C. impunctatus* might avoid woodland and then the wood would tend to act as a barrier to the free passage of midges. Fortunately there were two gaps in the wood, both associated with lines of drainage, in which presumably the trees had failed to survive in wet acid soil.

The larger gap was near the road and centred on a tributary of the Joppa burn. Here the wood was very sparse over a width of 230 yd. and with a gap

50 yd. wide in which there were no trees (Pl. XIII, fig. 1). The other break was about a quarter of a mile further south along the wood. The gap in the trees was much smaller and the wood was sparse over 100 yd. with a treeless gap of about 30 yd. (Pl. XIII, fig. 2). Joppa Wood is separated from the Muir by a boundary wall, which bounds Bogfield and Field X on that side, and the wood may, therefore, from the point of view of siting of traps, be regarded as part of these fields, although in Field X there is a wide ditch between the wood and the open pasture.

A further difficulty arose in measuring flight range from Brunston Muir in that it did not form a single uniform breeding site. *C. impunctatus* breeds in

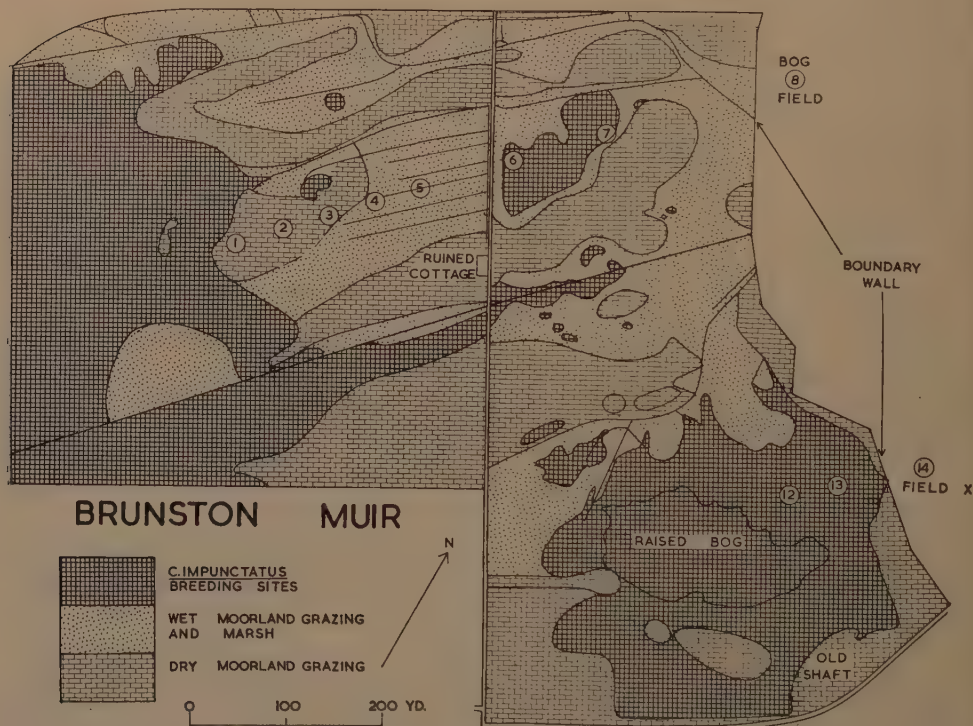


Fig. 3.—Detail of ecological zones on eastern half of Brunston Muir. Joppa Wood, not delineated, lies to the right of the boundary wall. Extension of breeding sites into the gaps in the wood, around traps 8 and 14, are not shown.

bogland soils in association with *Sphagnum* spp. and *P. commune*. A large part of the Muir was composed of bogland in which *Sphagnum* abounded in association with *Eriophorum vaginatum* and a small amount of heather (*Calluna vulgaris*). Elsewhere this association gave way to a fresh-water marsh community where there was no *Sphagnum* and the cotton grass was replaced by *Juncus articulatus* and other rushes. The drier area was colonised mainly by grasses. Therefore, it became essential to map the various plant associations before deciding on the precise location of the trapping lines.

From the point of view of the present studies, interest centred on the eastern half of the Muir because of the prevailing south-westerly wind. There were

two large areas of bogland available here, one south of Walstone farm and the other north of the old mine shaft in the south-east corner of the Muir. South of Walstone farm a large area of raised bog, now much eroded, stretched away to the west for a quarter of a mile. It did not extend east of the farm but the edge of the bog led away to the south in a broad sweep to join a tongue of bogland which passed eastwards to the south of the ruined cottage (fig. 3). The north-eastern corner of the Muir, delimited by this bogland curve, consisted largely of grassland and contained only relatively small scattered patches of ground potentially suitable for breeding of *C. impunctatus*.

It was decided to run a long line (A) of traps from the eastern edge of the bogland straight towards the middle of the large gap in Joppa Wood. Traps were erected at 0, 50, 100, 150, 200, 300, 400, 600, 800, 1,000 and 1,200 yd. from the bog. The first five traps (0–200 yd.) were west of a path, the sixth (300 yd.) just east of the path, on the edge of another possible source of *C. impunctatus*. The seventh (400 yd.) was to the leeward of this additional breeding site and it was expected that this would be reflected by an increase in the size of catches on this trap. The last four traps were off the Muir and placed in a very wet field known as Bogfield. Although this field was very wet there was very little *Sphagnum* except in the gap in the trees where trap no. 8 (600 yd.) was erected. After trap 9 (800 yd.) it was necessary to alter the bearing of the line of traps by 23 degrees to avoid crossing the road (A 766), and entering an arable field where the growing crops might influence catches. Therefore the line was continued in Bogfield parallel to the road and 14 yd. inside the field. The last trap (no. 11 at 1,200 yd.) was placed 18 yd. west of a copse of young trees. The traps in Bogfield were in fact nearer to a breeding site to the north but there was a hill in between and flight to the traps would be at right angles to the prevailing wind.

It was a distinct advantage to be able to utilise a breeding site which presented such a broad front to the prevailing wind, because it meant that the wind could change its direction quite appreciably and still be blowing from the breeding site to the traps. Also, with midge movement taking place on a broad front, observations would be less influenced by dilution, since, except at the edges, the losses and gains by lateral movement, in a broad band of wind-borne midges, would on the average cancel each other out.

Like most rough moorland grazing in Scotland, Brunston Muir carried ewes and lambs at low density, while Bogfield contained no livestock until the last week when four young calves were grazed there.

In the south-east corner of the Muir there was a large area of breeding which converged on the smaller gap in Joppa Wood. Here there was a well-defined edge to the bogland, which extended into the gap in the wood but no further. This gap was smaller (Pl. XIII, fig. 2) and the possibility of the wood acting as an obstacle to movement of *C. impunctatus* was greater. As a check on this eventuality two traps of line B were erected on the breeding site itself at distances of 50 and 100 yd. from the boundary wall, or – 90 (trap 13) and – 140 yd. (trap 12) from the edge of the breeding site. Trap 14 (0 yd.) was erected in the gap and 40 yd. east of the wall. The next four traps (15–18) were placed 50, 100, 150 and 200 yd. from trap 14 in a line across a grassy pasture field. There were some marshy patches in the field but no suitable breeding sites for *C. impunctatus*. This field (X) carried a herd of young heifers and bullocks during the early weeks of observation but was then left empty. Traps 19 and 20 at 400 and 600 yd., respectively, continued the line into the next field (Y) which was occupied by milking cows. This field also had marshy patches but none suitable for *C. impunctatus*. The last trap in this series was placed in the garden of Brunston cottage at a distance of 750 yd. from the edge of breeding.

TABLE II.
Seasonal variations in catches of *Culicoides* between 27th May and 7th July 1958.

Week no.	Date	<i>C. impunctatus</i>		<i>C. pulicaris</i>		<i>C. punctatus</i>		<i>C. delta</i>		<i>C. obsoletus</i> group		<i>C. pallidicornis</i>		<i>C. picipennis</i>		Other spp.		Total
		♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
1	27 May-2 June	9	1	11	100	12	40	4	24	1	3	0	0	0	0	0	0	205
2	2-9 June	110	57	30	307	8	32	7	62	7	41	0	0	2	6	0	0	669
3	9-16 June	1108	728	38	359	3	48	24	40	7	112	4	7	1	11	0	0	2490
4	16-23 June	1569	2019	6	357	7	16	6	21	21	143	4	18	0	2	0	0	4189
5	23-30 June	3712	8741	13	374	1	29	19	16	13	301	17	56	0	0	0	0	13292
6	30 June-7 July	699	1352	9	106	2	4	2	11	8	113	8	44	1	2	0	5	2366
	Total ..	7207	12898	107	1603	33	169	62	174	57	713	33	125	4	21	0	5	23211

Method of trapping and analysis.

The adult population was estimated by means of sticky traps. Each trap consisted of a metal cylinder—12 inches long and 5 inches in diameter—around which was wrapped a sheet of celluloid coated with 'Stopmoth', a proprietary tree-banding grease. The cylinders were painted black and supported on wooden stakes with the centre of the long vertical axis six ft. above the ground.

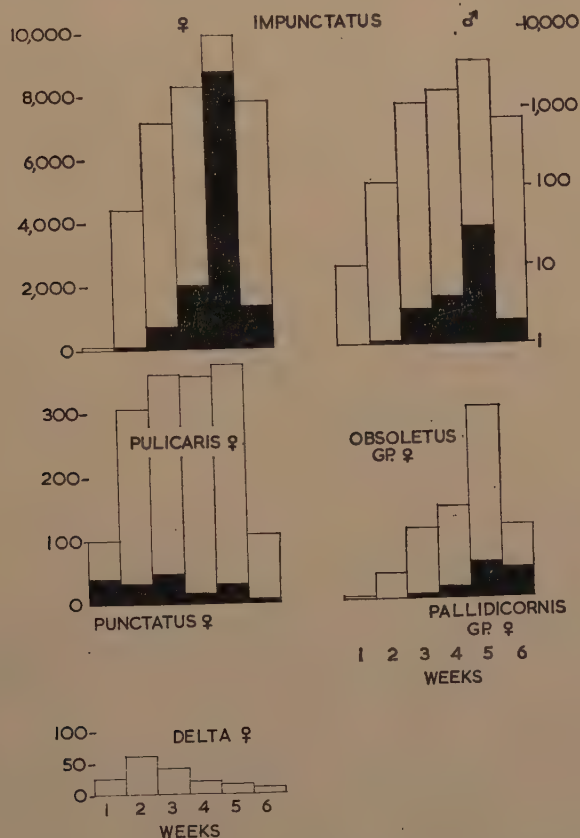


Fig. 4.—Abundance of adults of *Culicoides* species during period of observation (27th May to 7th July). In the top histograms, solid and open columns represent numbers of *C. impunctatus* on an arithmetic and logarithmic scale, respectively, females on the left, males on the right. In middle histograms, solid columns indicate *C. punctatus* and *C. pallidicornis*, respectively.

The celluloid sheets were changed weekly, the specimens of *Culicoides* removed, rendered grease-free by treatment with equal parts glacial acetic acid and ethyl acetate on a water bath, and preserved in 70 per cent. alcohol. Trapping was continued for six weeks from 27th May until 7th July 1958. The traps were exposed for seven days on each occasion except the first when the traps were only up for six days.

The results obtained are set out in Table II and fig. 4. Of the 23,211 specimens of *Culicoides* identified, 20,105 or 86.6 per cent. were of *C. impunctatus*.

The other species collected were *Culicoides pulicaris* (L.), *C. punctatus* (Mg.), *C. delta* Edw., *C. obsoletus* (Mg.) group, *C. pallidicornis* Kieff. and *C. pictipennis* (Staeger), but, of these, only *C. pulicaris* and the species of the *C. obsoletus* group were collected in sufficient numbers for analysis. In view of the composite nature of the latter it was valueless to attempt any analysis.

The number of females of *C. pulicaris* remained remarkably constant during the middle four weeks of the observations. In contrast to this the numbers of both sexes of *C. impunctatus* showed rapid changes from week to week. So great are these fluctuations that arithmetically the series is dominated by one week, the fifth, in which more than half the males and two-thirds of the females of *C. impunctatus* were captured. The overwhelming influence of this one week can be minimised by working with the logarithm of the catch (compare the solid and open histograms at the top of fig. 4). C. B. Williams (1947) has shown that for many biological investigations a logarithmic transformation is suitable. Since there is no logarithm for zero it is usual to work with $\log_{10}(n + 1)$ where n represents the catch.

The transformed data were subjected to an analysis of variance in which the variance was separated into three components: (1) that due to seasonal changes in population (obviously the largest contribution to the over-all variance); (2) that attributable to differences between the traps, which is a measure of the change in population density with distance from the breeding site, and is the part in which we are most interested; and (3) there is the residual variance or experimental error which is an estimate of the effect of all the many uncontrolled variables including those more usually regarded as experimental errors. From this can be calculated the statistic $t_{0.05, \bar{x}}$ which gives the 5 per cent. fiducial limits of the mean. The 5 per cent. limit for the difference between any pair of means is $Qs_{\bar{x}}$ using the appropriate value of Q , which can be obtained from Snedecor (1956, Table 10.6.1).

In the logarithmic analysis the figures used were correct to three places of a decimal although in the tables given later the means are given to two places only, which is adequate for purposes of comparison but not for analysis.

As so few midges were caught in the first two weeks (27th May–9th June) these findings have been incorporated with those of the third week (9th–16th June). The main effect of this will be to reduce the seasonal variance but this is unimportant in the present study.

In some cases the analysis has also been made on the original arithmetical data. The results of the arithmetical and logarithmic analyses were in general agreement.

Another method of reducing the domination of one week over the next is to express the catch on each trap as a percentage of the weekly total. This enables ready comparison to be made between the same trap in different weeks and consistency is readily appreciated. This method has been used in the histograms given later. It is not a satisfactory basis for analysis because all the weeks count equally, which ignores the added reliability of the weeks with large catches.

Wind direction.

The experiments were designed to take advantage of the prevailing south-westerly winds. No records of wind direction were made on the site during the experiment but most of the early preparation was carried out in a strong south-westerly wind. The nearest meteorological observation stations to the site are (1) Blyth Bank, $7\frac{1}{2}$ miles SSE., (2) West Linton, $4\frac{1}{2}$ miles SW., (3) Penicuik, 3 miles ENE., and (4) Bush House, 5 miles NE. These stations make only single daily observations on wind speed and direction at 10 a.m. (British Summer Time). There are several difficulties about relating these observations directly

to the midge catches. Firstly, 10 a.m. is not the optimum time for midge activity, and secondly, these are spot readings so that the wind may change direction markedly during the rest of the day. In addition there are considerable differences between the observations of the four stations. Thus, during the 42 days of the experiment, the wind directions of the four stations differed by over 90° on 12 occasions, by 90° on 14 days and by less than 90° on 16 days, while general agreement was reached on only two days.

The dispersal of *C. impunctatus* is not solely dependent on wind direction but also on wind speed. The midges are active at low wind speeds (Beaufort scale 0, 1 and possibly 2) when the air movement is insufficient to move a wind vane (5 m.p.h.). Even then other meteorological factors, *e.g.*, light, must not be limiting if flight is to occur. These considerations must be borne in mind when assessing the relevance of wind-direction data. The pooled daily wind-direction observations of the four stations are:—

Calm	N.	NE.	E.	SE.	S.	SW.	W.	NW.	Total
8	7	29	28	38	7	37	7	7	168

There is a predominance of winds from NE. to SW. through SE., but many of these winds were too strong for midge activity. The distribution of those winds with Beaufort scale values of 0 and 1 (*i.e.*, wind 0–3 m.p.h.) were:—

Calm	N.	NE.	E.	SE.	S.	SW.	W.	NW.	Total
8	4	19	12	12	5	20	3	5	88

There is still a dominance of easterly winds (NE.–SE.) and it must be accepted during the consideration of the trapping results that the flying population might have been subject to more easterly winds than anticipated.

TABLE III.

Catches of females of *C. impunctatus* on the 11 traps of line A.

Week number	Number of trap and its distance from breeding site (yd.)											Total
	1 0	2 50	3 100	4 150	5 200	6 300	7 400	8 600	9 800	10 1000	11 1200	
1–3	21	20	20	14	18	12	18	15	22	16	24	200
4	38	76	41	38	39	43	46	36	40	41	34	472
5	160	184	185	300	197	240	216	73	95	78	88	1816
6	42	37	44	42	42	49	45	16	18	17	18	370
Arithmetic total	261	317	290	394	296	344	325	140	175	152	164	2858
Arithmetic mean	65	79	73	99	74	86	81	35	44	38	41	
Logarithmic mean	1.69	1.76	1.72	1.72	1.70	1.71	1.74	1.47	1.56	1.50	1.54	$t_{0.05}^s \frac{s}{\bar{x}}$ ± 0.14

See text for meaning of $t_{0.05}^s \frac{s}{\bar{x}}$, and Table II for the actual period covered by the weeks.

Results.

Line A, traps 1–11, Brunston Muir and Bogfield.

The observations on females of *C. impunctatus* are recorded in Table III and fig. 5. None were caught in the first week of observation and only 21 in the

second so that the data for weeks 1-3 are virtually those of the third week (9th-16th June) when almost 90 per cent. of the total for these weeks was captured (179 out of 200).

It was intended that line A should throw light on the dispersion of *C. impunctatus* from a large breeding site. It was anticipated that numbers would drop for 300 yd. and then be increased by the additional breeding site between the 300- and 400-yd. traps (see fig. 3). A further small increase might occur at 600 yd. due to breeding in the gap in the wood. The picture obtained was quite different. In weeks 1-3 and 4 there was hardly any difference between the catches at the edge of the breeding site and at 1,200 yd. In the other two weeks (5 and 6) there was a lower catch on the traps at 600 yd. or more. The bottom histogram in fig. 5 is a measure of consistency and is the average of the percentages given in the upper four histograms.

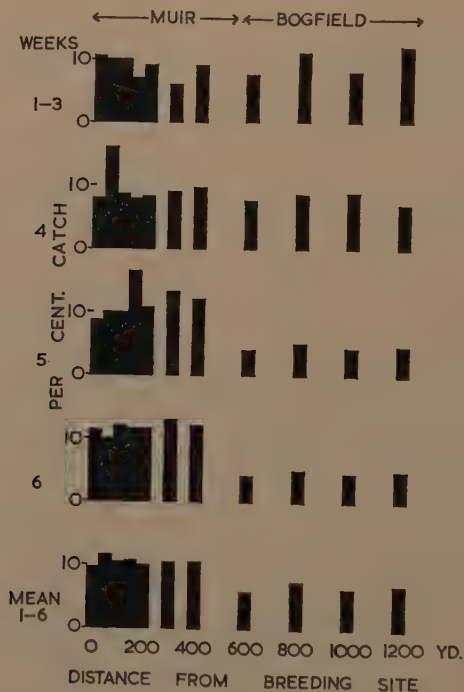


Fig. 5.—Weekly catch of females of *C. impunctatus* on traps of line A as a percentage of total catch in week.

The first striking feature of these results is the absence of a regression of density with distance. The catches fall into two groups, those from 0-400 yd. and those from 600-1,200 yd. This grouping is equally evident in the arithmetic and logarithmic means (Table III). It is not obvious that this drop between 400 to 600 yd. is to be interpreted as a measure of flight range. One would have expected this to have manifested itself by a more or less steady decrease in number, not a sudden single step-like drop from one level to another (10 per cent. to $6\frac{1}{2}$ per cent.). This drop occurs at the passage from Brunston Muir to Bogfield, all those on the Muir (traps 1-7) being in the high group and those

in Bogfield (traps 8-11) in the low one. These data are analysed in Table IV, (a). There is a very highly significant difference between these weeks as was expected. The differences between the traps were just significant ($P < 0.05$). But when this analysis of the trap differences is carried further it is found that the difference between Bogfield and the Muir is very highly significant and the differences between traps in the same field significantly smaller than expected.

The interpretation to be placed on this result is not clear. In theory the residual must have the smallest mean square because all the other estimates contain not only the residual but may also include another additional source of

TABLE IV.

Analysis of variance of catches ($\log_{10}(n+1)$) of females of *C. impunctatus* on traps of line A.

Source of variance	Degrees of freedom	Sum of squares	Mean square	F	F _A
(a) Traps 1-11					
Weeks ..	3	4.827543	1.609181	89.808***	38.560***
Traps ..	10	0.452524	0.045252	2.525*	1.483
fields ..	1	0.418807	0.418807	23.373***	12.583***
traps ..	9	0.033717	0.003746	1/4.783*	1/4.003*
Residual ..	30	0.537551	0.017918		
Total ..	43	5.817618			
(b) Traps 1-7, Brunston Muir					
Weeks ..	3	4.055190	1.351730	160.385***	
Traps ..	6	0.013404	0.002234	1/3.773	
Residual ..	18	0.151703	0.008428		
Total ..	27	4.220297			
(c) Traps 8-11, Bogfield					
Weeks ..	3	1.137443	0.379148	164.418***	
Traps ..	3	0.020313	0.006771	2.936	
Residual ..	9	0.020758	0.002306		
Total ..	15	1.178514			

*, ** and *** indicate probabilities of equal or less than 0.05, 0.01 and 0.001, respectively. F_A indicates F value obtained when analysis based on original arithmetic data.

variation. The result in Table IV, (a) is, therefore, unusual because the residual variance is significantly ($P < 0.05$) larger than the between-traps (same field) variance. This suggests that the residual variance contains in addition to the expected experimental error a component which is inflating the real experimental error. The factor responsible for this increased variance must fulfil certain conditions. Firstly, it must affect traps differently over the same period. If it operated similarly on all the traps at the same time it would have been incorporated with the seasonal variance (between weeks). But also, although over short periods it affects traps differently, over long periods it must affect all traps more or less equally so that it is not removed with the between-trap variance. These characteristics of the factor can be seen in fig. 5 where in week 4, trap 2 (50 yd.) had a very large catch and in week 5 the large catch occurred on trap 4 (150 yd.) and yet when the data are consolidated (bottom histogram) there is hardly any difference between the catches of the first seven traps (0-400 yd.).

The factor producing this differential effect on the traps could either be microclimatic or biotic. In this experiment all the traps were exposed three ft. or more above the herb layer on open moorland so that microclimatic differences between traps were likely to be slight. On the other hand, the main source of blood for the females of *C. impunctatus* would be the sheep grazing on the Muir, where they were present in low density, and, clearly, the presence of sheep near a trap at a time when the midges were active would increase the catch on that particular trap. If the sheep moved at random relative to the traps then they would be near different traps on the various occasions when midges were active.

The possibility of the presence of a host being the unknown factor can be pursued further. Bogfield had no domestic stock in it for almost the whole of the period of observation. (Four young calves appeared in the field during the last week.) The factor should be absent from the catches in this field. In Table IV, (b) and (c), the data for both the Muir and Bogfield have been analysed separately. In both there are highly significant differences between the weeks as expected. In Bogfield, however, the variance between traps is larger than the residual ($F = 2.936$). On Brunston Muir the variance between traps is still markedly smaller than the residual ($F = 1/3.77$) but this just falls short of significance ($P = 0.1$). This is due mainly to the fewer degrees of freedom available. Nevertheless, the analysis indicates that the residual contains an additional component on Brunston Muir to that on Bogfield. It seems reasonable to associate this with the presence of hosts as far as the boundary of the Muir at 550 yd.

In fig. 5 (weeks 1-6) it can be seen that there is no indication of a regression of midge density on distance on Brunston Muir (traps 1-7, 0-400 yd.). If that be so then the between-trap variance will provide another estimate of the experimental error. The residual here includes a host factor in addition to that of experimental error. In Bogfield there is no host factor and the residual should measure the experimental error. It is therefore interesting to note the agreement between these two estimates of experimental error. The Bogfield residual mean square is 0.0023 (Table IV, (c)) and that for trap mean square on Brunston Muir (Table IV, (b)) is 0.0022. Other comparisons can be made between the mean squares of Table IV, (b) and (c). Thus the F ratio between the two week mean squares is 3.565 with a possibility of 0.5 and between the trap mean squares it is 3.031 ($P = 0.2$). Both these comparisons indicate that the two sets of data could be drawn from the same population; but the two residuals differ significantly ($F = 3.655$ and $P = 0.05$), which serves to stress the fact that they are probably not drawn from the same population, or as suggested above one contains an additional component, probably host attraction.

From this evidence it would appear that the difference between Bogfield and Brunston Muir is not one of distance from the breeding site but presence or absence of suitable hosts.

The data for males of *C. impunctatus* are given in Table V and fig. 6. Their density does not appear to be dependent upon the proximity of the breeding site, and in fact the largest catch occurred on trap 7, 400 yd. away. In the analysis of variance (Table VI) there is the expected highly significant difference between the weekly catches and a significant difference between the traps. The latter can be attributed entirely to the difference between the fields. The variance between traps in the same field is of the same order as that of the residual (0.0206 of 0.0139). In other words there is no evidence of a host factor in the males, which is to be expected since the males do not feed on blood. Yet the males show the same drop in catch level between the Muir and Bogfield. In the female this was interpreted as a reduction due to the absence of hosts. In

addition there is a general agreement between the distributions of the two sexes. Thus, although the Chi-square tests on the numbers of each sex caught on the traps reveals highly significant differences between the two distributions ($\chi^2 = 52.109$; $P < 0.001$) this is entirely due to one trap (no. 4 at 150 yd.). When

TABLE V.

Catches of males of *C. impunctatus* on the 11 traps of line A.

Week no.	Number of trap and its distance from edge of bog (yd.)											Total
	1 0	2 50	3 100	4 150	5 200	6 300	7 400	8 600	9 800	10 1000	11 1200	
1-3	34	57	38	13	24	18	36	23	29	18	24	314
4	45	33	39	27	33	36	35	33	28	23	31	363
5	80	70	77	77	81	113	121	41	39	52	51	802
6	12	19	14	12	14	19	21	9	11	13	24	168
Arithmetic total	171	179	168	129	152	186	213	106	107	106	130	1647
Arithmetic mean	43	45	42	32	38	47	53	27	27	27	33	
Logarithmic mean	1.56	1.61	1.57	1.40	1.50	1.55	1.64	1.68	1.41	1.38	1.50	$t_{0.05}^s \bar{x}$ ± 0.12

For symbols see Table III.

this is omitted, there is no difference between the sex ratios on the other ten traps ($\chi^2 = 15.681$; $P = 0.10 - 0.05$). This can be summarised by stating that the distributions of the two sexes tend to be similar but not identical.

TABLE VI.

Analysis of variance of catches ($\log_{10}(n+1)$) of males of *C. impunctatus* on the 11 traps of line A.

Source	Degrees of freedom	Sum of squares	Mean square	F
Weeks	3	2.359301	0.786434	56.655***
Traps	10	0.352761	0.035276	2.541*
fields ..	1	0.167005	0.167005	12.031**
traps ..	9	0.185756	0.020639	1.486
Residual ..	30	0.416444	0.013881	
Total ..	43	3.128506		

For symbols see Table IV.

Line B, traps 12-21, Brunston Muir and farm.

The catches of females of *C. impunctatus* on the traps of line B are recorded in Table VII and given as percentages of the weekly catch in fig. 7. The

conditions under which these traps were exposed were extremely varied (see p. 467 for details) not only in their physical environment but also in the proximity of hosts. For example, traps 12 and 13 were sited on Brunston Muir with its low concentration of sheep; trap 14 was placed in the small gap in Joppa Wood. Between it and the field containing traps 15–18 there was a broad ditch, which would tend to keep cattle away. The cattle population in Field X changed during the experiment. There was a high density of cattle throughout week 2 but they were removed during week 3 and remained away for the rest of the experiment (Table I).

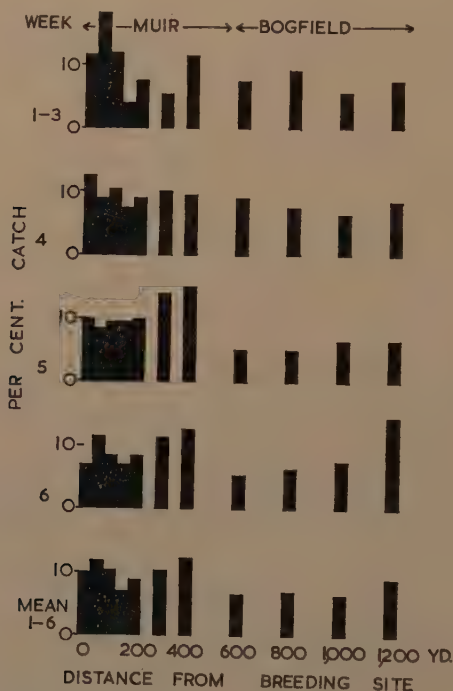


Fig. 6.—Weekly catch of males of *C. impunctatus* on traps of line A as a percentage of total catch in week.

The analysis of variance of these data is given in Table VIII. There is the usual highly significant difference between the weeks but none between the traps. It will be noted that the residual variance is high (0.0301). It has already been shown that in line A the experimental error on its own was only about 0.0023 but the host (sheep) factor increased it to 0.0084 (Table IV, (b), (c)). In line B there is not only a sheep factor on the Muir but a transitory cattle factor affecting traps 14–18, a permanent cattle factor on traps 19 and 20, and a human one on trap 21 in the cottage garden. (See Table I.) These additional sources of variation are incorporated in the residual.

When cattle were in Field X (fig. 7, weeks 1–3), the highest catches of females of *C. impunctatus* were made in the middle of the field (traps 16 and 17) and few were to be found in Field Y. In week 4, immediately after the cattle were removed, the difference between the fields was less obvious but in week 5, when Field X had been empty for over a week, the positions were reversed—the traps

TABLE VII.

Catches of females of *C. impunctatus* on the ten traps of line B.

Week no.	Number of trap and its distance from edge of bog (yd.)										Total
	12 -140	13 -90	14 0	15 50	16 100	17 150	18 200	19 400	20 600	21 770	
1-3	22	23	16	7	36	32	16	12	9	16	189
4	51	52	27	45	51	41	27	31	26	42	393
5	158	102	53	61	70	57	80	175	150	129	1035
6	38	17	35	23	15	21	20	14	13	25	221
Arithmetic total	269	194	131	136	172	151	143	232	198	212	1838
Arithmetic mean	67	49	33	34	43	38	36	58	50	53	
Logarithmic mean	1.72	1.59	1.49	1.43	1.58	1.56	1.48	1.51	1.44	1.60	$t_{0.05}^s \bar{x}$ ± 0.18

For symbols see Table III.

in Field Y making higher catches. In week 6, the midges were more concentrated near the Muir and it is interesting to note that in this week the wind was from the east on all but the last day. Out of the 28 wind observations for this week, 25 were NE. to SE., one was S. and two only were SW. It would appear that wind was the responsible factor for the pattern of distribution in this week.

TABLE VIII.

Analysis of variance of catches ($\log_{10}(n+1)$) of (a) females, (b) males of *C. impunctatus* on the ten traps of line B.

Source	Degrees of freedom	Sum of squares	Mean square	F
(a) Weeks ..	3	3.186071	1.062024	35.260***
Traps ..	9	0.274975	0.030553	1.014
Residual ..	27	0.813257	0.030120	
Total ..	39	4.274303		
(b) Weeks ..	3	3.735995	1.245332	38.937***
Traps	9	1.452331	0.161370	5.045***
Muir v. rest	1	1.055600	1.055600	33.005***
Traps ..	8	0.396731	0.049591	1.550
Residual ..	27	0.863543	0.031983	
Total ..	39	6.051869		

For symbols see Table IV.

It will be noticed that trap 19 (400 yd.) always caught more specimens than trap 20 (600 yd.). Perhaps this is a hint of a density/distance regression, but it should be noted that the existence of a permanent source of food (the inhabited cottage) was sufficient to produce an increase in the catch on the most distant trap (no. 21, at 750 yd.) in all except week 5.

The highest catch is made on trap 12, the one farthest out on the Muir, but trap 13, the other one on the Muir, is not distinguishable from the rest. This suggests that the wood does not in itself present a barrier to female midge dispersal.

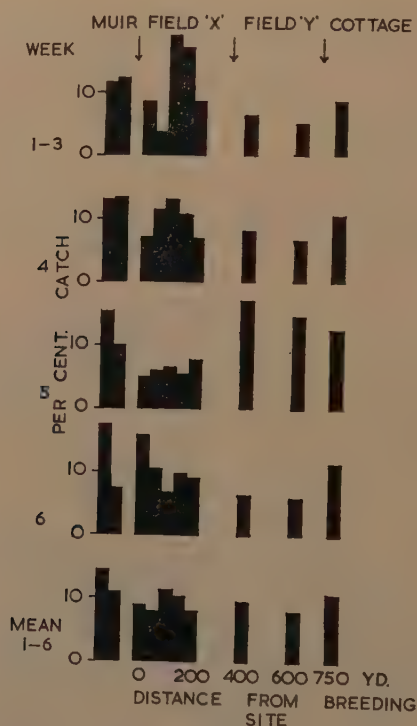


Fig. 7.—Weekly catch of females of *C. impunctatus* on traps of line B as a percentage of total catch in week.

The catches of males of *C. impunctatus* are recorded in Table IX, illustrated in fig. 8 and analysed in Table VIII. There is a highly significant difference between the traps. It is clear from the data that the two moorland traps catch more midges than the others. In fact the analysis of variance shows that the whole of this difference can be attributed to that between the Muir traps and the rest. The explanation of this observation is not apparent. It could be that the wood acted as a barrier to the movement of males. It is interesting that here for the first time (cf. fig. 8, weeks 5 and 6, with fig. 1) there is a density/distance regression of the type anticipated and it also is associated with woodland. The wood did not act as a barrier to the females, and, as a result, a Chi-square test on the sexes being similarly distributed has a probability far smaller than 0.001. It is necessary to exclude not only traps 12 and 13, which have a high

percentage of males (48 and 57 per cent.), but also traps 19 and 20, with a low proportion of males (28 and 24 per cent.), before the Chi-square test indicates no significant difference.

When there are cattle in Field X, many males pass through the wood (fig. 8, weeks 1-3), but this passage declines in week 4 when the cattle have been removed, and in the succeeding weeks (5 and 6) relatively few males pass into

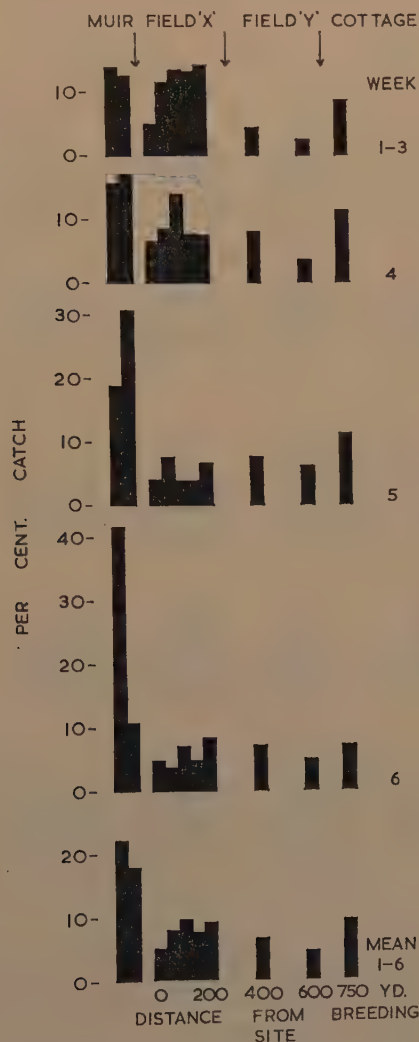


Fig. 8.—Weekly catch of males of *C. impunctatus* on traps of line B as a percentage of total catch in week.

Fields X and Y. This behaviour contrasts markedly with that of the females which passed into Field Y, presumably in search of a host and blood-meal (*cf.* week 5 in figs. 7 & 8). As with the females, trap 19 catches more than trap 20 and once again there is an increase in the catch on trap 21. This implies that

TABLE IX.

Catches of males of *C. impunctatus* on the ten traps of line B.

Week no.	Number of trap and its distance from edge of bog (yd.)										Total
	12 —140	13 —90	14 0	15 50	16 100	17 150	18 200	19 400	20 600	21 770	
1-3	41	37	15	34	40	39	42	13	8	25	294
4	63	68	27	35	57	31	30	32	14	46	403
5	103	168	23	42	21	21	37	41	33	61	550
6	35	9	4	3	6	4	7	6	4	6	84
Arithmetic total	242	282	69	114	124	95	116	92	59	138	1331
Arithmetic mean	61	71	17	29	31	24	29	23	15	35	
Logarithmic mean	1.75	1.66	1.18	1.33	1.39	1.29	1.40	1.28	1.09	1.43	$t_{0.05}^s \bar{x}$ ± 0.18

For symbols see Table III.

the males, like the females, have been attracted to the vicinity of the cottage. Since the males do not feed on blood they have no need of man or his stock as a source of food. They may, nevertheless, be attracted to hosts as a means of locating females for mating. Similar behaviour has been recorded for *C. nubeculosus* by Pomerantzev (1932).

TABLE X.

Catches of females (left side) and males (right side) of *C. impunctatus* on the five traps of line C.

Week no.	Trap no. and distance from breeding site (yd.)					Total	Trap no. and distance from breeding site (yd.)					Total
	22 0	23 50	24 100	25 150	26 200		22 0	23 50	24 100	25 150	26 200	
1-3	21	14	14	12	12	73	23	17	15	20	19	94
4	74	31	63	59	85	312	37	31	50	45	52	215
5	486	180	147	173	263	1249	90	71	104	164	85	514
6	43	43	59	74	56	275	20	24	41	50	20	155
Arithmetic total	624	268	283	318	416	1909	170	143	210	279	176	978
Arithmetic mean	156	67	71	80	104		43	36	53	70	44	
Logarithmic mean	1.89	1.65	1.73	1.75	1.80	$t_{0.05}^s \bar{x}$ ± 0.15	1.56	1.50	1.64	1.73	1.57	$t_{0.05}^s \bar{x}$ ± 0.12

For symbols see Table III.

Line C, traps 22-26.

These traps were arranged beside the wall separating two interconnecting fields containing cattle and sheep (Table I). The trapping results are given in Table X and fig. 9. An analysis of variance indicated the usual highly significant difference between weeks but an insignificant difference between traps ($F = 1.702$; $P = 0.2$ for females and $F = 2.590$; $P = 0.1$ for males). This is shown in Table X by the fact that in the females the greatest difference between

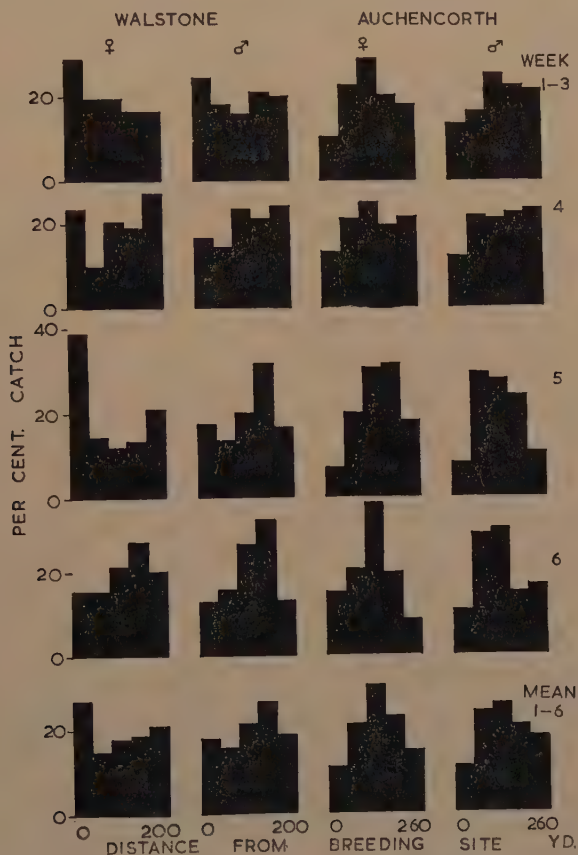


Fig. 9.—Weekly catch of males and females of *C. impunctatus* on traps of line C (Walstone) and line D (Auchencorth) expressed as a percentage of total catch in week.

trap means is 0.24 (traps 22 and 23) while to reach the 5 per cent. level of significance with five traps the difference ($Q_{\bar{x}}$) should be 0.31. In the males the relevant figures are 0.23 (traps 23 and 25) and 0.24 at the 5 per cent. level.

There is, therefore, no evidence of a decrease in midge density with increasing distance from the breeding site over a distance of 200 yd. This needs to be qualified by two other conditions of the experiment. Firstly, there were abundant hosts between the breeding site and the traps and secondly, flight took place in a

north-westerly direction, which would be at right angles to the normal south-westerly winds but would be helped by the easterly winds recorded during the experimental period.

Line D, traps 27-31 and line E, traps 32-36, Auchencorth farm.

The traps of line D extended from a bog to the farm around the edge of a pasture field which always contained a horse, a flock of rams and, on occasions, cattle. On the other side of the wall from traps 28 and 29 sheep were grazed, and adjacent to traps 30 and 31 was a pasture field which had cattle throughout the period of observation. The results for line D are given in Table XI and fig 9. Here for the first time the analysis of variance gave a highly significant difference between the traps for both sexes ($F \text{♀♀} = 7.026$; $F \text{♂♂} = 6.177$ $P < 0.01$). This is due to higher catches being made on the traps in the pasture field than on the breeding site or in the farm garden. This is probably related to host availability.

TABLE XI.

Catch of females (left) and males (right) of *C. impunctatus* on the five traps of line D.

Week no.	Trap no. and distance from breeding site (yd.)					Total	Trap no. and distance from breeding site (yd.)					Total
	27 0	28 65	29 130	30 195	31 260		27 0	28 65	29 130	30 195	31 260	
1-3	22	48	62	43	39	214	51	63	96	83	81	374
4	70	112	133	104	115	534	49	88	84	90	94	405
5	262	738	1129	1167	396	3692	107	403	378	325	148	1361
6	59	82	145	79	33	398	23	64	67	33	37	224
Arithmetic total	413	980	1469	1393	583	4838	230	618	625	531	360	2364
Arithmetic mean	103	245	367	348	146		58	155	156	133	90	
Logarithmic mean	1.85	2.13	2.29	2.16	1.95	$t_{0.05}^s \bar{x}$ ± 0.14	1.71	2.04	2.08	1.98	1.91	$t_{0.05}^s \bar{x}$ ± 0.13

For symbols see Table III.

On the breeding site, being rough grazing, there were only sheep at low density while there were cattle, sheep and a horse available in the pasture field. In addition the horse and rams used to rub against the posts supporting the traps and horse hair was often found on those traps. The farm garden, however, contained no animals and did not appear to be frequented much by man. It will be noticed that in both sexes the lowest catch is on the breeding site, the second lowest in the farm garden and the highest in the middle of the line, although the catches in the three pasture-field traps (28-30) are not statistically separable. Once again the distribution of hosts swamps any density/distance regression, and again the males show the same qualitative distribution as the females, suggesting that both are reacting to the same stimuli although not necessarily to the same degree.

Line E, which extended across one of the pasture fields, suffered much interference from animals, nevertheless the data obtained are given in Table XII. The results agree with those of line D, namely that the catch in the field was higher than that on the breeding site or in the garden, and that this is shown by both sexes.

Distribution of C. pulicaris.

The only other species of *Culicoides* captured in sufficient numbers to warrant analysis was *C. pulicaris* (females). Its breeding sites are distinct from those of *C. impunctatus*, and hence the traps are not arranged to measure or detect a

TABLE XII.

Catch of females (left) and males (right) of *C. impunctatus* on the traps in line E.

Week no.	Trap no. and distance from breeding site (yd.)					Total	Trap no. and distance from breeding site (yd.)					Total
	32 0	33 65	34 130	35 195	36 260		32 0	33 65	34 130	35 195	36 260	
1-3	32	—	22	38	17	<u>109</u>	38	—	44	50	20	<u>152</u>
4	57	—	—	164	48	<u>269</u>	42	—	—	87	35	<u>164</u>
5	249	—	—	475	200	<u>924</u>	92	—	—	276	110	<u>478</u>
6	54	—	—	—	30	<u>84</u>	29	—	—	—	37	<u>66</u>
Arithmetic total	392			<u>677</u>	295	1386	201			<u>413</u>	202	<u>860</u>
Arithmetic mean	98			<u>169*</u>	74		50			<u>103*</u>	51	
Logarithmic mean (weeks 1-5)	1.89			2.16	1.75		1.73			2.03	1.64	

— = trap knocked down.

Figures underlined are not complete.

* For calculation of mean, catch in week 6 assumed to be nil.

For other symbols see Table III.

density/distance regression. The breeding sites of *C. pulicaris* are in the wetter areas of marsh and swamp which occur in the lower-lying parts of pasture fields or at the edges of bog.

The population of *C. pulicaris* was low in the first week and then rose to a higher level, at which it stayed during the next four weeks before declining again in week 6 (see Tables II (which includes line E) and XIII (which excludes line E)).

On and around Brunston Muir the density of *C. pulicaris* was low but evenly distributed. This is shown by the absence of a significant difference between any of the means of traps 1-21. The greatest difference between means is 0.39 (0.75-0.36) compared with 0.72 for five per cent. significance. At Walstone farm (line C), where a suitable breeding site occurred at the edge of the bog, there was a significantly greater density of *C. pulicaris* (mean 1.10; compare 0.62 of A and 0.59 of B). Although the trap catches in C vary, none of the differences are significant, the largest being 0.43 (1.32 - 0.89), and $Qs_{\bar{x}} = 0.56$.

At Auchencorth farm (line D) the density is significantly lower than at

Walstone in spite of the existence of an apparently suitable breeding site in the same field as the traps, but it is higher than on Brunston Muir although not significantly so. At Auchencorth there is a significant difference between trap catches as there was in *C. impunctatus* although in this case it is only trap 31, the one in the farm garden, which has a low catch compared with traps 27-30.

TABLE XIII.

Summary of catches of females of *C. pulicaris* on traps of all lines except E.

Trap no.	LINE A										
	1	2	3	4	5	6	7	8	9	10	11
Arithmetic total	18	26	28	34	19	11	18	28	32	26	24
Arithmetic mean	3	4	5	6	3	2	3	5	5	4	4
Logarithmic mean	0.52	0.66	0.54	0.74	0.60	0.41	0.55	0.68	0.75	0.68	0.67

Trap no.	LINE B									
	12	13	14	15	16	17	18	19	20	21
Arithmetic total	15	13	14	12	23	48	54	45	35	23
Arithmetic mean	2	2	2	2	4	8	9	7	6	4
Logarithmic mean	0.48	0.46	0.49	0.36	0.65	0.71	0.66	0.75	0.74	0.61

Trap no.	LINE C					LINE D					All traps
	22	23	24	25	26	27	28	29	30	31	
Arithmetic total	259	118	60	51	119	61	73	74	45	14	1420
Arithmetic mean	43	20	10	8	20	10	12	12	7	2	45.8
Logarithmic mean	1.32	1.19	0.93	0.89	1.16	0.94	0.83	1.01	0.83	0.40	0.72 $t_{0.05}^s \bar{x}$ ± 0.28

		WEEKS						TOTAL
		1	2	3	4	5	6	
Arithmetic total	58	258	319	333	347	105	1420
Arithmetic mean	2	8	10	11	11	3	
Logarithmic mean	0.39	0.82	0.87	0.82	0.84	0.56	$t_{0.05}^s \bar{x}$ ± 0.12

		LINE				TOTAL
		A	B	C	D	
Arithmetic total	264	282	607	267	1420
Arithmetic mean	4	5	20	9	
Logarithmic mean	0.62	0.59	1.10	0.80	
$t_{0.05}^s \bar{x}$	± 0.09		± 0.13		

Sub-totals of weeks and lines included.

From these observations the impression was gained that the horse and cattle were particularly attractive to *C. pulicaris*. This would explain its relative absence from the farm garden (trap 31) and its low density on Brunston Muir (traps 1-13) and high density at Walstone (traps 22-26). At Brunston farm, cattle were present in Field X for part of weeks 1 and 3 and the whole of week 2 only, and 89/151 examples of *C. pulicaris* trapped on traps 14-18 were caught in week 2, also fair numbers were taken on traps 19 and 20 where cattle were always present.

Lastly, it should be noticed that there is considerable difference between the catches of the sexes of *C. pulicaris*. The sex ratio was 1♂:15♀ compared with *C. impunctatus* 3♂:5♀. This would suggest that the males of *C. pulicaris* are either very short lived or behave differently from the females.

Discussion.

(a) Flight range and midge control.

It will be apparent that these experiments have failed to answer the question: How far will *C. impunctatus* fly over open country with the help of the prevailing wind? In fact no evidence was found of a density/distance regression. It is pertinent to ask why these results are so different from those obtained at Bannachra. At Bannachra, flight range was measured through woodland where there would be no wind to assist dispersal, which would have to be made by unaided flight. Also Bannachra was remarkably deficient in animal life. There were no domestic animals on either experimental site, although sheep grazed the heather moor above the site. In addition, wild mammals and birds were scarce; there was therefore little host attraction to encourage flight.

In places like Bannachra, one wonders how *C. impunctatus* obtains sufficient blood to maintain its population. There are many similar localities, isolated islands, remote moors, where the midge population appears to be far larger than the available wild life is able to support. A similar problem is presented by the biting flies of the subarctic wastes, and Hocking (1952) has shown that at least one species (*Aedes communis* (Deg.)) is autogenous, autolysing its flight muscles to mature eggs. In *Culex pipiens molestus* Forsk., only a small percentage of females in wild populations are autogenous (Knight, 1951). It is possible that some individuals of *C. impunctatus* are also autogenous. W. L. Nichols (private communication) reports finding fully developed ova in females of *C. impunctatus* which had had no blood-meal. The population could be maintained by those that find a blood-meal near the breeding site and those that are autogenous. The rest of the population would be surplus and disperse outwards in search of a blood-meal and other suitable breeding sites. It is doubtful whether they would return to the same site. In this way the range of the species would be constantly enlarged or maintained at its maximum.

This dispersion would presumably be at random in sheltered areas such as Bannachra Wood, or downwind in the open, until *C. impunctatus* becomes aware of the presence of hosts. Then movement would cease to be aimless and would be directed towards the host, causing pockets of higher midge density to be built up in the vicinity of potential hosts. Such concentrations were shown by traps 28 to 30 of line D in a pasture field (Table XI) and by trap 21 in the cottage garden (Table VII).

There are hardly any data available on the distance over which biting flies perceive a host and proceed directly to it. There is much information on the stimuli which promote feeding when the host and insect are in close proximity, but very little on the distances from which a biting fly is aware of the presence of a host. The only reference I have found concerns observations of Napier Bax (1937, quoted by Buxton, 1955) on *Glossina swynnertoni* Aust. He found that they could see oxen at 150 yd., and in the absence of vision could sense a

party of men and oxen 60 yd. away. However, this information is not readily applicable to such tiny creatures as midges.

The Bannachra results are still valid for the conditions under which they were obtained, absence of wind carriage and lack of hosts to stimulate activity, but unfortunately these conditions are not obtained where control measures are needed. Buildings inhabited by man are an attraction to midges and this is increased when domestic animals are grazed in the vicinity although there is no information as to whether the grazing animals satisfy more midges than they attract and thereby act as a barrier between man and the midge. In addition, most midge-infested places are open to the wind and wind-borne invasions will be likely.

These observations must change our conception of midge control as an individual responsibility. No longer can one think of an individual protecting the environs of his home against *C. impunctatus* by dealing with all the breeding sites within 200 yd. Now it must be expected that infestations will come from sources three-quarters of a mile or more away, especially in the direction of the prevailing wind, and these sources are likely to be on another person's land. This raises the status of the problem from an individual to a communal responsibility. A control scheme now will require the co-operation of many interested persons. This may be achieved by local voluntary organisations or perhaps it should be accepted as a public-health responsibility. It is true that *C. impunctatus* does not transmit any disease to man, but neither does the bed-bug, *Cimex lectularius* L., yet the latter is accepted as a public-health responsibility. Surely it is not unreasonable to suggest that the midge problem is the rural counterpart of the urban bed-bug problem.

This investigation has emphasised the difficulty or impossibility of measuring midge density as an isolated phenomenon since the density is dependent upon the presence of suitable hosts. Equally, flight range cannot be examined in isolation since it is affected not only by the position of the breeding site and the direction of the prevailing wind but also by the presence or absence of hosts between the breeding site and the observer.

This means that every control scheme will have to be designed especially to meet local conditions. On the credit side it should be pointed out that as the larvicide remains effective for at least three years (Kettle, Parish & Parish, 1959) it will be possible to extend the treated area in the light of experience without having to respray the whole area.

The greater flight range demonstrated here will substantially increase the area requiring treatment and consequently the cost of control. This will render it too expensive for isolated habitations surrounded by extensive breeding sites but where there are more houses and the terrain more varied the expense should not be prohibitive although the actual cost will depend upon the precise conditions.

In view of the records of variations in wind direction from the SW. it cannot be assumed that dispersion was less in other directions from the breeding sites. This point should be checked by further observations in all directions from a breeding site.

The greater flight range clears up a number of disquieting observations when midges were observed more than 200 yd. from obvious breeding sites, and brings the dispersal of *C. impunctatus* more into line with the suggestions of Dorsey (1947) that *C. pcliliouensis* Tokunaga may fly two miles, and of R. W. Williams (1951) that *C. tristriatulus* Hoffman may fly five miles, in both cases with the help of the wind. Nicholas (1953), working with *C. grahamii* Aust., found that the population decreased to 1/10th for every 370 yd. distance from the breeding site. This gives a flight range about six times greater than that found earlier for *C. impunctatus* (Kettle, 1951). Hill (1947), also working with *C. impunctatus*, found a much smaller flight range of about 300 yd.

(b) *Dispersion of males of C. impunctatus.*

In this paper, evidence has been presented to show that males of *C. impunctatus* tend to collect in the vicinity of hosts or near inhabited cottages although it is not known whether this is in response to the host or to the females which in turn are responding to the host. However, the males and females do not have precisely the same distributions. They show certain qualitative similarities but are quantitatively distinct.

Two general patterns of sexual behaviour have been described in *Culicoides*. In one, the males form small discrete swarms and pairing occurs in the vicinity of the swarms (Downes, 1955). In the other, sexual recognition occurs on contact. Two species exhibit this in captivity in small tubes, and Pomerantzev (1932) has described this in nature for *C. nubeculosus* where copulation occurred while the female was sucking blood. For this to occur, the males need also to respond to the presence of a host, which is the type of behaviour ascribed above to males of *C. impunctatus*.

Clearly, the frequency with which these two patterns of sexual behaviour occur in a species or population will affect the number of males caught on a trap. If swarming predominates, then the male movement will be very restricted, since swarms usually form over a fixed marker. Consequently the catch of stationary traps will be low, unless they are used as markers, because the male's movements are mainly oscillations over a marker.

On the other hand, if sexual recognition is by contact, then the male must follow the females in their search for a host. It would be an advantage for small creatures to have a rendezvous in the vicinity of or on the host.

This difference in mating behaviour may explain the varied sex ratios recorded by the same trapping technique in different places. Kettle (1955) has shown that on emergence the sex ratio in many species of *Culicoides* is the normal 1:1, yet trapping results very rarely approach this figure (see Table II and fig. 4). At Bannachra, Kettle (1951) obtained 58 per cent. males on sticky traps. In the present study, males form 36 per cent. of the total catch of *C. impunctatus*. At Talladale the percentage was even lower. This difference has long been considered to be due to some change in male behaviour, but without being able to specify in what way the behaviour had changed. Here is a suggestion which should be investigated further.

Summary.

In the summer of 1958, experiments were conducted in the vicinity of Brunston Muir, Midlothian, 11 miles SE. of Edinburgh, to measure the flight range of *Culicoides impunctatus* Goetgh. from its breeding site in the direction of the prevailing south-westerly wind. Thirty-six sticky traps were exposed for six weeks from 27th May to 7th July and captured 23,211 specimens of *Culicoides*, of which 20,105 were of *C. impunctatus* (7,207 males and 12,898 females).

Eleven of the traps were arranged in a line over 1,200 yd. The catch of females did not alter for 400 yd., then decreased to a new level which remained constant from 600 to 1,200 yd. This decrease was associated more with the absence of livestock after 550 yd. than with any density/distance regression. The male distribution was similar to that of the females.

Ten more traps stretched over 750 yd. and again no regression was discernible. The female distribution was affected more by the availability of hosts than distance from the breeding site. The male distribution here was different. They appeared to pass less readily through a gap in a narrow belt of woodland than did the females.

Five traps arranged at right angles to the prevailing wind over 200 yd. recorded no difference in female or male catches over this distance. However, in this

experiment, there were abundant hosts available in the vicinity of all five traps, and during the period of observation the wind showed considerable deviation from the normal south-westerly direction.

Ten more traps were arranged in two parallel lines between a breeding site and a farm 260 yd. away. There was an increase in the catch of both sexes in the middle of each row, where the traps were in a pasture field, due to the presence of domestic animals.

The relevance of these results to midge control is discussed, in particular the change in estimate of the flight range from 200 yd., which was formerly regarded as the practical limit of flight, to three-quarters of a mile or more. The flight range is dependent upon wind carriage and the availability of acceptable hosts on the way. If suitable hosts are found en route, few females of *C. impunctatus* fly further.

The observations on males of *C. impunctatus* are discussed from the point of view of male behaviour and also from their bearing on the explanation of variations in sex ratio which have been recorded among populations of *C. impunctatus* by use of the same technique.

The distribution of *C. pulicaris* (L.) over Brunston Muir and its environs is given. It was present in low density on the Muir but was more abundant in pasture fields containing large domestic animals.

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References.

- BUXTON, P. A. (1955). The natural history of tsetse flies.—*Mem. Lond. Sch. Hyg. trop. Med.* no. 10, 816 pp. London, H. K. Lewis.
- DORSEY, C. K. (1947). Population and control studies of Palau gnat on Peleliu, western Caroline Islands.—*J. econ. Ent.* **40** pp. 805-814.
- DOWNES, J. A. (1955). Observations on the swarming flight and mating of *Culicoides* (Diptera: Ceratopogonidae).—*Trans. R. ent. Soc. Lond.* **106** pp. 213-236.
- HILL, M. A. (1947). The life-cycle and habits of *Culicoides impunctatus* Goetghebuer and *Culicoides obsoletus* Meigen, together with some observations on the life-cycle of *Culicoides odibilis* Austen, *Culicoides pallidicornis* Kieffer, *Culicoides cubitalis* Edwards and *Culicoides chiopterus* Meigen.—*Ann. trop. Med. Parasit.* **41** pp. 55-115.
- HOCKING, B. (1952). Autolysis of flight muscles in a mosquito.—*Nature, Lond.* **169** p. 1101.
- KETTLE, D. S. (1951). The spatial distribution of *Culicoides impunctatus* Goet. under woodland and moorland conditions and its flight range through woodland.—*Bull. ent. Res.* **42** pp. 239-291.
- KETTLE, D. S. (1955). Sex ratios among British *Culicoides*.—*Proc. R. ent. Soc. Lond.* (A) **30** pp. 70-72.

- 0 203 KETTLE, D. S. & LAWSON, J. W. H. (1952). The early stages of British biting midges *Culicoides* Latreille (Diptera: Ceratopogonidae) and allied genera.—*Bull. ent. Res.* **43** pp. 421–467.
- 198 KETTLE, D. S., NASH, R. H. & HOPKINS, B. A. (1956). Field tests with larvicides against *Culicoides impunctatus* Goetgh. in Scotland.—*Bull. ent. Res.* **47** pp. 553–573.
- 5 128 KETTLE, D. S. & PARISH, R. H. (1957). Field trials of larvicides against *Culicoides* with a discussion on the relationship between rainfall and larval control.—*Bull. ent. Res.* **48** pp. 425–434.
- 7 77 KETTLE, D. S., PARISH, R. H. & PARISH, J. (1959). Further observations on the persistence of larvicides against *Culicoides* and a discussion on the interpretation of population changes in untreated plots.—*Bull. ent. Res.* **50** pp. 63–80.
- KNIGHT, K. L. (1951). A review of the *Culex pipiens* complex in the Mediterranean subregion (Diptera; Culicidae).—*Trans. R. ent. Soc. Lond.* **102** pp. 354–364.
- METCALF, R. L. (1955). Organic insecticides: their chemistry and mode of action.—392 pp. New York, N.Y. & London, Interscience Publ. Inc.
- NAPIER BAX, S. (1937). The senses of smell and sight in *Glossina swynnertoni*.—*Bull. ent. Res.* **28** pp. 539–582.
- NICHOLAS, W. L. (1953). The dispersal of *Culicoides grahamii* and *C. austeni* from their breeding-sites prior to their taking a blood-meal.—*Ann. trop. Med. Parasit.* **47** pp. 309–323.
- PARISH, R. H. (1958). An attempt to control *Culicoides impunctatus* Goetghebuer around human habitations in Scotland with observations on the flight range and ability of females to perceive a suitable host.—*Rep. Scot. Tourist Bd* no. 12.
- PARISH, R. H. & KETTLE, D. S. (1957). An attempt to control *Culicoides impunctatus* Goetghebuer with larvicides at Talladale, Loch Maree, Ross-shire, 1954–1956.—*Rep. Scot. Tourist Bd* no. 9.
- POMERANTZEV, B. I. (1932). Beiträge zur Morphologie und Anatomie der Genitalien von *Culicoides* (Diptera, Nematocera). [In Russian with German summary.]—*Mag. Parasit.* **3** pp. 183–214.
- SNEDECOR, G. W. (1956). Statistical methods applied to experiments in agriculture and biology.—5th edn., 534 pp. Ames, Iowa, Iowa St. Coll. Pr.
- WILLIAMS, C. B. (1947). The logarithmic series and its application to biological problems.—*J. Ecol.* **34** pp. 253–272.
- WILLIAMS, R. W. (1951). Observations on the bionomics of *Culicoides tristriatulus* Hoffman with notes on *C. alaskensis* Wirth and other species at Valdez, Alaska, summer 1949 (Diptera, Heleidae).—*Ann. ent. Soc. Amer.* **44** pp. 173–183.



FIG. 1. View from path on Brunston Muir looking east towards Bogfield through the large gap in Joppa Wood. Trap 6 can be seen in left foreground and trap 7 left of centre.



FIG. 2. View from Brunston Muir towards small gap in Joppa Wood and Field X. Traps 12 and 13 are seen in centre.

THE BIOLOGY OF TWO SPECIES OF MOSQUITO, *MANSONIA AFRICANA*
(THEOBALD) AND *MANSONIA UNIFORMIS* (THEOBALD),
BELONGING TO THE SUBGENUS *MANSONIOIDES*
(DIPTERA, CULICIDAE).

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CONTENTS	PAGE
Distribution of the two species	492
Interfertility of strains of <i>M. uniformis</i>	493
Cross-fertility of <i>M. africana</i> with <i>M. uniformis</i>	495
Feeding and biting behaviour	495
Oviposition	497
Reactions to water surface	497
Reactions to background of breeding place	498
Reactions to organic pollution	499
Reactions to leaf surface	501
Length of adult life	502
Eggs and hatching	503
Attachment of the larvae and pupae	504
Moulting and length of life-cycle, metabolism	507
Emergence of the adult	510
Discussion	511
Summary	512
Acknowledgements	513
References	513

A number of aquatic insects obtain their oxygen by piercing the submerged parts of aquatic plants. This habit has been recorded in various beetles (*Donacia*, *Lissorhoptrus*; Varley, 1937) and in the flies of the genera *Erioptera*, *Chrysogaster* and *Notiphila* (Varley, 1959) and the mosquitos of the genera *Ficalbia* and *Mansonia* (= *Taeniorhynchus*) (Iyengar, 1935). Only species of *Mansonia* are the vectors of human disease. The adult mosquitos, belonging to the subgenus *Mansonioides*, are well-known vectors of human filariasis caused by *Wuchereria malayi* (Brug & de Rook, 1930) and, also, may be important vectors of *Wuchereria bancrofti* (Brygoo, 1957; de Rook, 1957; van Dijk, 1958; Toumanoff, 1958). These mosquitos also transmit other species of *Wuchereria*, and of *Dirofilaria*, infecting domestic and wild animals (Buckley & Edeson, 1956; Buckley, Nelson & Heisch, 1958; Gunewardene, 1956; Wharton, 1959a). Both in the subgenus *Mansonioides* and in the subgenus *Coguillettidia* the adult mosquitos are possible vectors of virus diseases (Philip, 1930; Daubney & Hudson, 1933; Howitt & others, 1949; Kokernot & others, 1957). Despite the importance of *Mansonia* in the transmission of disease, relatively little has been recorded about the biology of these mosquitos. This has been due mainly to the difficulties of discovering the larval and pupal stages in the field, and to difficulties in maintaining laboratory colonies of the mosquitos. Most of the collected information on the biology in the field has been given by Carter (1950) and Mattingly (1957), and by Haddow (1942, 1945, 1954), Haddow, Gillett & Highton (1947) and Gillett (1957) with special

reference to the biting and oviposition behaviour. Jayewickreme & Niles (1952) and Wharton (1957) have described methods for rearing *Mansonioides* in the laboratory and, in London, three species of *Mansonioides* have been maintained for one or more years (Laurence & Smith, 1958). During the maintenance of these colonies it has been possible to study and compare the biology of two species which often occur together in Africa, *M. africana* (Theo.) and *M. uniformis* (Theo.).

Distribution of the two species.

The world distribution of *M. africana* and *M. uniformis* is shown in fig. 1. The two species differ in the adult stage in the colour and distribution of the scales on the scutum and legs, and also in the structure of the male and female genitalia (eighth sternite), but are otherwise very similar. *M. uniformis* is found from 40°N. in east China (Feng, 1938), south through Cambodia, Thailand and Malaya to India and Ceylon, and then through the Seychelles Islands (Mattingly & Brown, 1955), to Africa. Eastwards, *M. uniformis* extends into Japan, across Java, Borneo and New Guinea, to Australia and the Solomon Islands. *M. africana* is restricted to the continent of Africa.

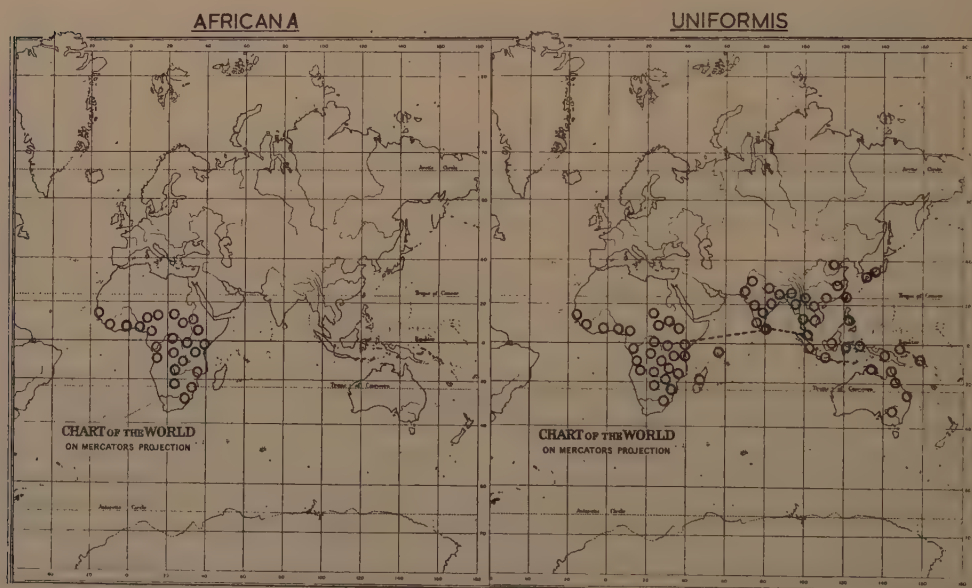


Fig. 1.—Maps showing the distribution (compiled from various sources) of *M. africana* and *M. uniformis*. The dotted line connects populations of *M. uniformis* shown to be interfertile in the laboratory.

In Africa, *M. africana* and *M. uniformis* are the only representatives of the subgenus *Mansonioides*, and both species are found from Senegal and the Sudan in the north, south to Bechuanaland, Moçambique and Natal. In West Africa, in Nigeria, Philip (1931), Beeuwkes & others (1933), Kerr (1933) and Mattingly (1949) found *M. africana* to be the commoner species, both in houses and at tree platforms, and this species was found to be commoner than *uniformis* in bungalows at Accra, in Ghana, by Macfie & Ingram (1916) and also in the breeding places in the Gambia (Laurence, 1959). Schwetz (1930) considered

M. uniformis as the commoner species in Central Africa, with *M. africana* abundant in certain localities, and *M. uniformis* is reported to be the commoner species in Angola (Gândara, 1956) and in the Sudan (Lewis, 1945). In East Africa, *M. africana* is the commoner species at tree platforms in Uganda (Haddow, 1945) and also in huts (Haddow, 1950), although both species show very similar biting habits. There is some evidence that the distribution of *M. uniformis* does not coincide completely with that of *M. africana*, as Haddow (1945) found *uniformis* scarce in the forest except at the extreme edges and in the vicinity of water, but more abundant in plantations. Smith (1955) found both species to be equally common on Ukara Island, Tanganyika, but suggested that *M. africana* was more abundant during the dry season and *M. uniformis* more abundant during the rains. In Kenya, Haddow (1942) found more *M. uniformis* entering huts, and van Someren, Heisch & Furlong (1958) also record a preponderance of *M. uniformis* in exit traps on the Kenya coast, although *M. africana* was collected more frequently by net catches out of doors. There is, therefore, some evidence that the ecological and seasonal distribution of the two species in Africa may not completely coincide. Estimates of the relative abundance of the two species must, therefore, be interpreted with caution. The present paper, comparing the biology of the two species, derives its comparisons largely from laboratory observations which exclude some of the difficulties in determining biological differences under field conditions.

Interfertility of strains of *M. uniformis*.

Both species are stenogamous and mate readily in small 25-cm.-cube cages. Mating takes place frequently between newly emerged adults less than 24 hours old and may take place even in test-tubes. Stationary females on the walls of the mosquito cages may be surrounded by four, or even six, males, all attempting to copulate. Males have also been observed trying to mate with dead females on the floor of the cage. Mating in the air has not been observed although, as recorded by Tate & Vincent (1936) in *Culex pipiens molestus* Forsk., frequent matings follow disturbance of the mosquitos in the cages. Antonipulle, David & Karunaratne (1958) found more mating activity in *M. uniformis* on moonlit nights, which suggests that the mating reaction is primarily a visual response. Females recently gorged on blood may attract males, and males mating with blood-fed females have also been observed by Jayewickreme (1953) in the field. On the other hand, females copulating with males may come to feed successfully on blood. Gillett (1957), with reference to the biting cycle of *M. africana*, has reviewed the relationship between mating and feeding in mosquitos, concluding that these reactions are not mutually exclusive. Females have been observed to reject males, usually by movements of the hind legs, and these females have been assumed to have already mated. Living sperm may still be present in females isolated from males for 20 days, and these females lay fertile eggs despite the long isolation. Mattingly (1957) refers to swarming in *Mansonioides*. This has not been observed in the laboratory. Jayewickreme (1953) observed mass matings, four hours after sunset, but did not observe the type of behaviour normal for swarming mosquitos.

The principal breeding colonies studied in the laboratory have been a colony of *M. africana* originating from Entebbe, Uganda, and a colony of *M. uniformis* from Kuala Lumpur, Malaya. Colonies of *M. africana* from Amani, Tanganyika, and of *M. uniformis* from Colombo, Ceylon, and Entebbe, Uganda, have also been maintained. It was of some interest to see if members of the colonies of *M. uniformis* from Malaya, Ceylon and Africa were interfertile, and also to see if the two species, *M. africana* and *M. uniformis*, interbred in the close confinement of the laboratory.

Attempts to cross-breed members of the colonies of *M. uniformis* from Malaya, Ceylon and Africa have all been successful; some viable offspring were produced from each cross experiment attempted. Mating between males and unmated females took place in the normal laboratory cages. There was, however, some evidence of a reduction in fertility of eggs in the crosses (c-e), between the African strain and the other strains maintained in the laboratory (Table I); and there was a marked reduction of fertility of eggs produced by the F_1 hybrids

TABLE I.

Fertility of matings of members of some colonies of *M. uniformis*.

Cross	Average no. of larvae/egg-mass from cross (expected 100)	Percentage of hybrid larvae from cross reared to adult	Average no. of larvae/egg-mass laid by hybrid F_1 females (expected 100)	Notes on fertility
(a) Malayan ♂ x Ceylon ♀	134.5	50%	39.4	Half of the egg-masses laid by hybrid F_1 females completely infertile. F_2 generation emerged.
(b) Ceylon ♂ x Malayan ♀	58.8	21%	90.2	F_2 generation emerged.
(c) Malayan ♂ x African ♀	40.7	33%	11.4	Egg-masses laid by hybrid F_1 females largely infertile (see text).
(d) African ♂ x Malayan ♀	14.5	37 larvae preserved (43%)	—	All egg-masses laid by Malayan ♀♀ fertilised by African ♂♂ largely infertile.
(e) Ceylon ♂ x African ♀	10.7	56%	8.3	Egg-masses laid by African ♀♀ fertilised by Ceylon ♂♂, and egg-masses laid by hybrid F_1 females, largely infertile.
(f) African ♂ x Ceylon ♀	—	Not attempted	—	—

from two of these crosses ((c) Malayan ♂ x African ♀ and (e) Ceylon ♂ x African ♀). This reduced fertility was most apparent in the cross (c) Malayan ♂ x African ♀ where, out of 17 egg-masses laid by the hybrid females, 6 were completely infertile, and the masses that hatched produced only 4, 6, 8, 9, 12, 13, 16, 23, 29, 30 and 43 larvae, respectively, when the normal expected number was 100 larvae per egg mass. One of the infertile egg-masses was laid by a hybrid female with living sperm in the spermatheca. The unhatched eggs either contained partially developed larvae, or showed no development at all. In the reciprocal cross (d), all the egg-masses laid by African females mated with Malayan males were largely infertile. A similar reduction of fertility was found in the cross (e) Ceylon ♂ x African ♀. There was also an apparent reduction in the fertility of eggs laid by the hybrids from the cross (a) Malayan ♂ x Ceylon ♀, but the reciprocal cross (b) did not show this. Despite the reduced fertility of

the hybrids of some of these crosses, the hybrid generations, when tested, were found to produce some offspring. *M. uniformis* therefore appears to be, at present, a valid species through its range from Africa to Malaya, although there is evidence of infertility between the more isolated populations.

Cross-fertility of *M. africana* with *M. uniformis*.

Attempts to cross *M. uniformis* (Malaya) with *M. africana* (Entebbe) have not been successful. In these experiments, unmated females were enclosed in 10 × 6 cm. glass cylinders for 24 hours with males of the opposite species. Under these conditions females kept with males of the same species are inseminated and lay fertile eggs. Six experiments, involving 33 males of *africana* with 19 females of *uniformis* and 68 males of *uniformis* with 30 females of *africana*, were continued for 24 hours or more and then the females were dissected. Males were seen repeatedly to attempt mating with females of the opposite species which were feeding, but the males were rejected by movements of the females' hind legs. No sperms were found in the spermathecae of any females from these interspecific crossing experiments, nor were any fertile egg-masses laid by females kept for three or more days. On one occasion a successful mating was observed, lasting for 30 minutes, between a male of *africana* and a female *uniformis*. This female, on dissection, was found to contain no sperms in the spermathecae, despite the prolonged period of mating. As the males will attempt to mate with one another, and even with dead mosquitos, the breaking down in a confined space of an apparent mating barrier is not wholly surprising. These experiments suggest that the two species are reproductively isolated and that occasional varieties found in the field are not due to hybridisation between the two species.

Feeding and biting behaviour.

The pattern of feeding in both *M. africana* and *M. uniformis* in the laboratory and in the field is very similar. In the laboratory, males and females feed readily on sugar solution on a cotton-wool pad and on fruit, such as apples and raisins. Lewis (1947), in the Sudan, observed females of *M. uniformis* sucking at the flowers of frangipani. Females that have the crop full of sugar solution may feed on blood but usually the females coming to bite have not recently fed on sugar or fruit. In the laboratory, females of both species have fed readily on the blood of man, cat, rabbit and guinea-pig. In the field, the species of *Mansonioides* are notorious biters of man although Haddow (1942), Carter (1950) and Smith (1955) have all found that more females are attracted to cattle. Smith (1955) also records blood-meals of *M. africana* and *M. uniformis* from fowl, bat, hyrax, goat and dog. In the tree canopy, Haddow & Dick (1948) found more females attracted to human bait than to monkeys. This predominant attraction to mammals in *Mansonioides* is in contrast to the behaviour of some African species of *Coquillettidia* which feed mostly on birds (Williams, Weitz & McClelland, 1958).

The females feed for the first time usually 24 hours after emergence (fig. 2) and then feed again as soon as possible after each oviposition. This readiness to feed immediately after oviposition accounts for the nuisance of these mosquitos when they are disturbed in the swamps. Old females, starved for 17 days, have also fed on blood. During feeding, clear droplets of fluid are deposited from the anus and the increase in weight is about, or just over, the weight of the mosquito feeding (2.4 + mg.). Females in cages, both mated and unmated, will feed readily during the day or night, but in the field most biting activity is at night (Haddow, 1945; Haddow, Gillett & Highton, 1947; Gillett, 1957) in the tree canopy, and also in native huts (Haddow, 1942). The biting activity in the field, except near the breeding places, is probably inhibited

by unfavourable microclimatic conditions during the day. The biting behaviour of *africana* and *uniformis* recorded by Haddow and his co-workers (*op. cit.*) shows that the two species have very similar biting habits in the field, although van Someren, Heisch & Furlong (1958) have suggested that there was some difference in the biting cycles of the two species on the Kenya coast. In this connection, *M. africana* in Uganda has shown maximum biting activity at all periods of the night (Haddow, 1954). Probably both young and old females

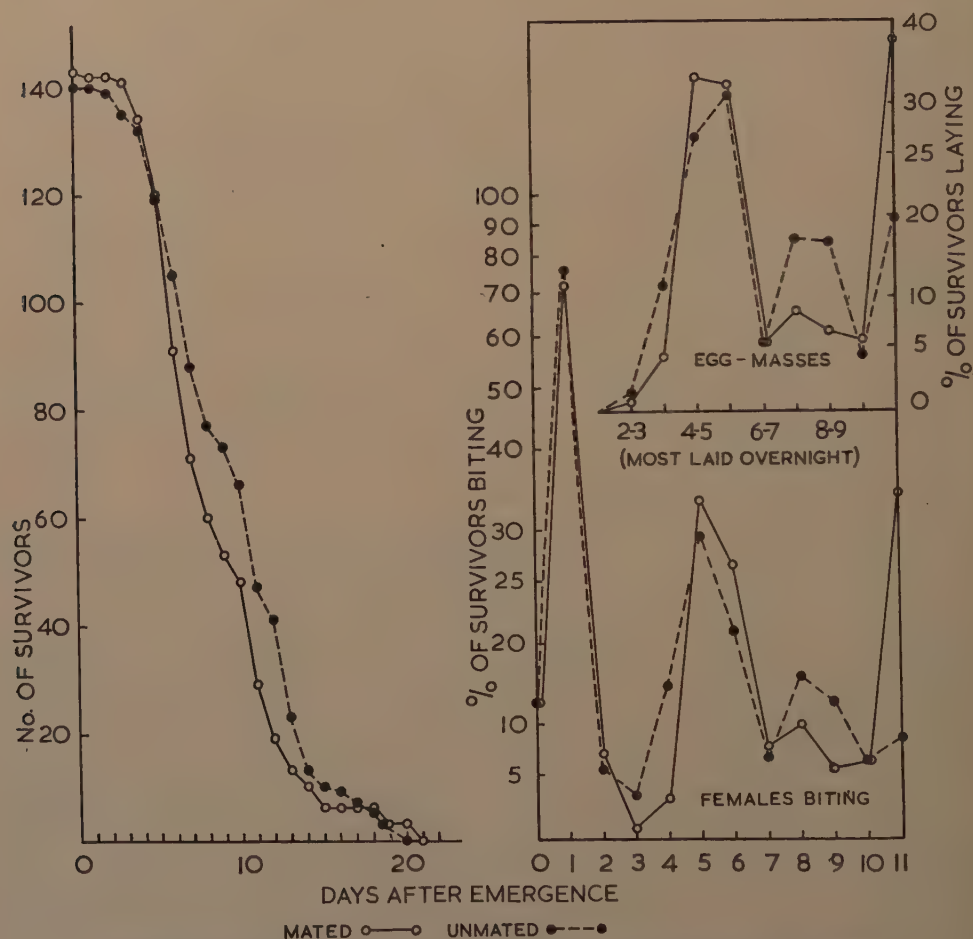


Fig. 2.—Survival of mated and unmated females of *M. africana* kept over floating leaves at 25–29°C., periodicity of biting and periodicity of oviposition.

feed throughout the night (Gillett, 1957), although Mattingly (1949) suspected the presence of two biting populations of *africana* in the tree canopy in Nigeria.

In the laboratory, there is a difference in activity between the two species immediately after feeding; the gorged females of *M. uniformis* are more difficult to catch for the normal colony transference to 'nursery' cages (Laurence & Smith, 1958) than the females of *M. africana*. This difference in activity after feeding was further tested in the following way. About 50 gorged females of one species at a time were transferred into a small box, 9 × 9 × 7 cm., with

a single 4-cm.-square exit hole, inside a larger 25-cm.-cube cage draped with damp lint and with an external polythene cover. The cage and box were arranged so that the aperture of the box faced an east window, and the mosquitos were left overnight. On the following morning, 16–17 hours later, the number of females that had emerged from the box into the cage and the number left in the box were counted. Out of 560 females of *africana* placed in the box, 334 (59%, range 43–80%) remained in the box, whereas out of 465 females of *uniformis*, 314 emerged leaving only 151 (32%, range 17–47%) behind in the box. This difference in activity may account for the preponderance of *M. africana* found indoors by Lewis (1947) in the Sudan and in huts in the Gambia (D. H. Murphy, personal communication) although here the species are on the edge of their range. Smith (1955) records a greater preference in *M. africana* for resting in dark places in Tanganyika, although Haddow (1942) suggested that both species did not rest for long in huts in Kenya.

Oviposition.

The biting and oviposition cycles (fig. 2) are closely related (see also Haddow & Gillett, 1958) but, in the laboratory, the two cycles can be put out of phase. Normally the females of *M. africana* and *M. uniformis* lay their eggs three to five days after the blood-meal, at 25–30°C. Christophers' Stage III of ovary development is reached within 48 hours of the blood-meal, Stage IV in 48–72 hours, and the eggs are normally laid four days after the blood-meal (fig. 2). Ovary development is more rapid in some individuals than in others. The remains of the previous blood-meal may still be found in the gut 72 hours after feeding. Females that have just laid eggs are immediately ready to feed again. Should the gravid females be prevented from laying, they can be persuaded to feed again, despite the presence of fully developed eggs in the abdomen. In one experiment, 16 females each of *M. africana* and *M. uniformis* were fed fully on human blood and were then offered human blood every day after this. All the females fed again four or five days later, but not before. The twice-fed females were then placed with floating leaves of *Salvinia* for oviposition (Laurence & Smith, 1958). Some of the females attempted to lay immediately, although their abdomens were grossly distended by the blood-meal. This suggests that the release of the inhibition from biting in *Mansonioides* is normally synchronised with the ovulation cycle, but is not dependent on it (Lavoipierre, 1958).

Reactions to water surface.

The eggs of *Mansonioides* are laid in compact masses on the undersides of floating leaves. When the females of *Mansonia africana* and *M. uniformis* are placed on a surface of leaves floating on water, the first reaction, if the females are going to lay, is a dipping movement of the proboscis. The females then begin to walk over the alternating leaf and water surface, regularly dipping the proboscis and touching the surface of the leaves and water between them. When the proboscis has located a small area of water the abdomen then curls forwards beneath the thorax, and this is followed by an attempt to push the abdomen downwards and backwards beneath the leaf. The curling forward of the abdomen may take place over a leaf; the females will then try to push the abdomen down through the leaf. As soon as the abdomen comes into contact with the water, it is then pushed downwards and backwards, and the female then takes up her final position for oviposition with most of the abdomen submerged and the rest of the body above the leaf (Iyengar, 1938; Laurence, 1959). During oviposition, the female moves the tip of her abdomen from one side to the other, at the same time gradually withdrawing her abdomen from the water. In this way a compact mass of eggs is formed a short distance from the edge of the leaf. The same sequence of events follows when females are

placed over small discs of paper, or cork, floating on the water. The initial dipping reaction of the proboscis has also been observed when gravid females came into contact with a thin film of water at the bottom of a glass container. This suggests that close proximity to the water surface provides the initial stimulus and that an alternating pattern of dry surfaces and water provides the environment for oviposition to be completed.

Reactions to background of breeding place.

In the field, there is evidence that females of both *M. africana* and *M. uniformis* are attracted by floating leaves shaded by taller vegetation growing in the water,

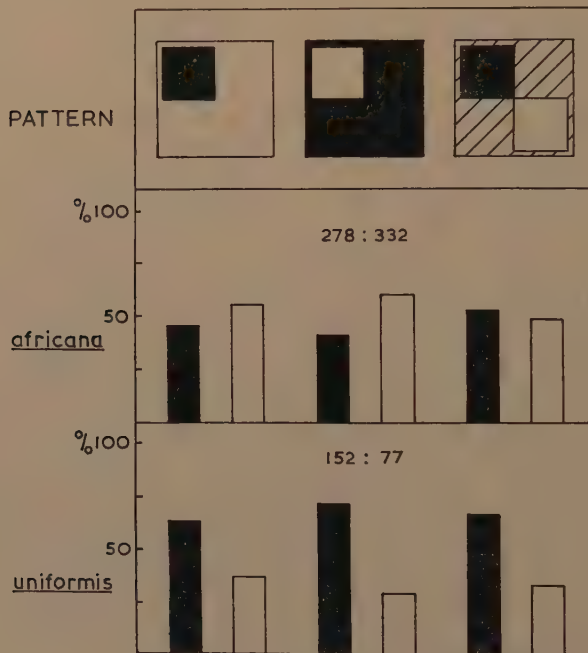


Fig. 3.—Relative numbers of egg-masses of *M. africana* and *M. uniformis* laid on dark (black columns) and light (white columns) backgrounds. The pattern of the background on the floor of the cage is shown above the columns. Total number of egg-masses laid on dark and light backgrounds is also given for each species.

and that leaves floating in open water are not attractive (Laurence, 1959). This suggested that the females might be attracted by the background of the emergent vegetation contrasted against the open water.

Alternative sites for oviposition were set up inside the laboratory cages, consisting of two petri dishes in which were floating *Salvinia* leaves, one petri dish being placed on a white, and one on a black, background. The position of the background in the cage was altered at each experiment. During the experiment only the top of the cage was covered by damp lint and the sides of the cage were uncovered. Three types of background pattern were used: a white square on a black background, a black square on a white background, and white and black squares on a neutral background (fig. 3). Gravid females

were introduced into the cages, always in the same position in the insectary, and left for 24-48 hours; the dishes were then removed and the egg masses in each dish counted. With *M. uniformis*, in 12 out of 13 experiments, more egg-masses were laid in the dish over a dark background (fig. 3) and a total of 152 egg-masses were laid over the black squares, compared with 77 laid over the white squares. The pattern of the background did not affect the result. No similar selection could be shown with *M. africana*. Females of this species laid more egg-masses on the dark background in eight experiments, and more egg-masses on the white background in ten experiments, and a total of 278 egg-masses were laid over the black squares compared with 332 egg-masses laid over the white squares. This difference between the two species may be due to a greater visual sensitivity in females of *M. uniformis* under the conditions of low light intensity inside the mosquito cages. Under field conditions, both species were found to select oviposition sites shaded by emergent vegetation (Laurence, 1959).

Experiments to simulate field conditions, by surrounding one of two petri dishes, containing *Salvinia*, by turf or by gauze strips hanging from the roof of the cage, have shown no selection of breeding site under these conditions. It was possible that a breeding site surrounded by grass, or by strips of gauze, would provide resting places for the females, from which they would be attracted downwards to the water below. Females of *M. africana*, provided with a choice of such a breeding site, and a petri dish containing *Salvinia* in the open, laid 40 egg-masses on *Salvinia* in the dish surrounded by gauze strips, and 54 egg-masses on the *Salvinia* in the open. The position of the dishes was reversed at each of four experiments.

Reactions to organic pollution.

The two species differ also in their sensitivity to water pollution. Iyengar (1938) found *M. annulifera* (Theo.) in Travancore, India, breeding mainly in pools polluted by coconut husks, and was able to show that clean pools deliberately contaminated with coconut husks or cow dung then became attractive to the gravid females of this species. The females also selected dirty water in preference to clean water in experiments in the laboratory. It has been assumed that all species of *Mansonioides* are attracted to polluted breeding places. Actually, in the laboratory, both *M. uniformis* and *M. africana* select clean water (tap water) in preference to the infusion of guineapig faeces used for culturing the larvae.

The reactions to water pollution have been tested by introducing gravid females into the apparatus shown in fig. 4, which consisted of a 3.5-cm.-diameter plastic tube, of over-all length 95 cm., turned down at each end. Each end of the tube was placed in a 150-cc. beaker containing water or polluted water at various concentrations of pollution, and a few leaves of *Salvinia* were provided to float inside each end of the tube. Female mosquitos were introduced into the apparatus at a point half-way between the ends of the tube and, after 24-72 hours, the number of egg-masses laid in each beaker was counted. Twenty to thirty mosquitos were used at each experiment. When tap water was provided in one beaker, and stock infusion of guineapig faeces at the other, females of both *M. africana* and *M. uniformis* laid more egg-masses on *Salvinia* leaves floating on tap water (fig. 4). When the tap water was replaced by guineapig infusion diluted to $\frac{1}{4}$ and $\frac{1}{8}$ the original stock concentration, *M. africana* continued to lay significantly more egg masses in the less polluted water but *M. uniformis* was unable to distinguish between them. Neither species was able to distinguish between the grossly polluted concentrations of the stock solution and a solution diluted to $\frac{1}{2}$ the original concentration.

An infusion of pellets of guineapig diet, D 18, is also used as a stock larval infusion and this was also used to produce degrees of pollution to test the reactions of the mosquitos at oviposition. Females of *M. africana* showed a greater sensitivity to D-18 pollution and significantly more egg-masses were laid in the $\frac{1}{2}$ and $\frac{1}{8}$ dilutions compared with the undiluted stock infusion. Females of *M. uniformis* did not distinguish between even the lowest $\frac{1}{8}$ dilution and the stock infusion (fig. 4).

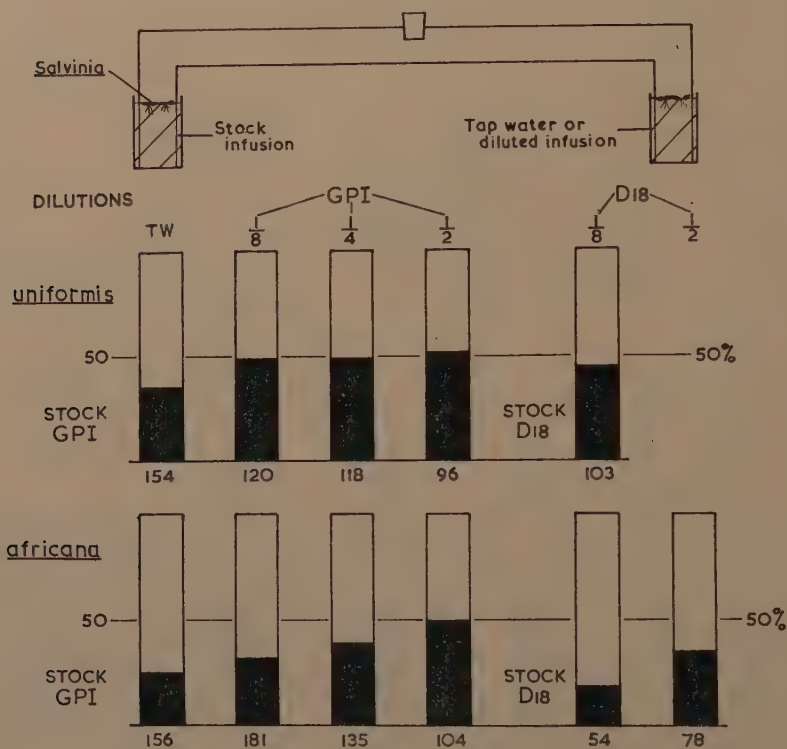


Fig. 4.—Relative numbers of egg-masses laid by *M. uniformis* and *M. africana* in tests comparing the attractiveness of polluted waters. The apparatus used is illustrated above. The percentages of egg-masses laid in the stock infusions are shown in black and the percentages laid in tap water (TW) or diluted infusion (GPI or D 18), as indicated above, in white. Total number of egg-masses laid is given below the columns for each species.

Fresh stock infusion, 4-8 days old, was used at each experiment and analyses of three of these infusions are given in Table II. The D-18 infusions contained more organic matter than did the infusion of guineapig faeces, and females of *M. africana* showed a more marked avoidance of the stock D-18 infusion, but this was not shown by *M. uniformis*. There is no obvious direct relationship between single factors, such as the Tidy figure, shown in Table II, and the results of these experiments with the two species. The laboratory experiments have, however, confirmed Hopkins' observation (1952) that *M. africana* showed a "slightly more marked preference" for clean water than did *M. uniformis* in Africa.

Reactions to leaf surface.

The females of *Mansonioides* will lay their eggs on the undersides of a variety of leaves (Bonne-Wepster & Brug, 1939; Carter, 1950). In the Gambia, West Africa (Laurence, 1959), the position of the leaf relative to the vegetation surrounding it appeared to be more important in the selection of leaves for oviposition than the species of leaf or its size. It is possible, in the laboratory,

TABLE II.

Analyses of stock infusion used in experiments on the effect of water pollution on oviposition.

Basic infusion	Organic carbon	Kjeldahl nitrogen	Biochemical O ₂ demand	O ₂ absorbed permanganate (Tidy figure)	NH ₃	NO ₂ NO ₃
Guineapig-faeces infusion nine days old	54	16.0	30	35	9	2
Guineapig-faeces infusion three days old	38	17.0	22	28	10	3
Diet-18 infusion seven days old	290	26.2	513	56	8	3

[Figures in parts per million.]

to show that some plant species are more acceptable for oviposition than others. Three small plants with floating leaves, *Salvinia*, *Lemna* and *Azolla*, were available for the experiments and on each occasion equal areas of two of the plants were provided in the oviposition jars for 10–20 gravid females. The results are given in Table III. The females of both species of *Mansonioides* prefer to

TABLE III.

Laying preferences on plants in the laboratory.

	Plant species		
	<i>Salvinia</i>	<i>Lemna</i>	<i>Azolla</i>
	No. of egg-masses		
<i>M. africana</i> {	136	61	—
	70	—	2
	—	21	8
<i>M. uniformis</i> {	112	56	—
	49	—	10
	—	23	5

lay on the leaves of *Salvinia*, and on *Lemna* leaves in preference to those of *Azolla*. The selection of *Salvinia* may be due to the different ways the leaves float on the surface. Both *Lemna* and *Azolla* float flat on the surface film, but in *Salvinia*, owing to the keeled shape of the leaf, the underside meets the surface of the water at an angle. During oviposition the abdomen of the female mosquito would more normally follow the slope of a leaf at an angle to the surface than one floating horizontally. Another habit of *Salvinia* that may facilitate

oviposition on this plant is that the leaves float with a comparatively large area of water surface between them. On such a surface a female quickly discovers a site suitable for oviposition. The leaves of *Lemna* float close together with little water surface exposed between the leaves, and females of *Mansonioides* have been observed trying unsuccessfully to break through small areas of surface film exposed between the leaves. Only relatively few places between the leaves are large enough to be suitable for oviposition. However, if isolated leaves of *Salvinia* are floated amongst *Lemna*, most egg-masses are again laid on the leaves of *Salvinia*, which suggests that the angle at which a leaf floats on the surface may influence oviposition more than the pattern of the leaves at the surface.

Leaf size is also important, as relatively few egg-masses can be found in the field on the larger leaves, more than 12 cm. in diameter (Laurence, 1959). This suggests that, in nature, the females search only a limited area at the water surface when attempting to oviposit. Also equal-sized leaves floating in small pools attract markedly different numbers of ovipositing females, and this may be due to the position of the leaf in the pool. It may also be due to females being attracted to leaves on which females have already laid, or are in the process of laying. In the laboratory, equal-sized discs of paper, 1 cm. in diameter, have been floated in the oviposition jars and a record has been kept of the numbers of egg-masses laid by females of *M. uniformis* on each disc. In 14 tests, 14 discs of paper were available for oviposition at each test, and a total of 509 egg-masses was laid on the discs. The distribution of the egg-masses on the equal-sized discs in the laboratory approximates to a negative binomial distribution (fig. 5), suggesting that there is no evidence of aggregation of egg-masses on discs in certain positions in the laboratory. There is evidence, however, that the distribution of egg-masses on the leaves in the field is not random and that aggregation may occur on certain leaves (see fig. 5). From these experiments it seems probable that, in the field, females are not attracted more to leaves being used by other ovipositing females, but that some leaves are in relatively unattractive positions.

Length of adult life.

Bertram & Samarawickrema (1958) have provided a method for determining the age of wild-caught females of *Mansonioides* by dissection of the ovaries and examination for follicular relics (*corpora lutea*). Wharton (1959b) has recorded wild-caught females coming to bite in Malaya which had oviposited at least three times, but females parasitised by *Wuchereria* of about the same apparent age had oviposited only once. This difference in apparent age might be due to the presence of filariae in the thoracic flight muscles restricting normal activity in the parasitised females. It is known that the females come to bite over a mile from the breeding places (Laurence, 1959) and some time may therefore elapse between oviposition and the next blood-meal. Vincke (1959) has recently shown, by marking and recapture experiments, that females of *M. uniformis*, in the Congo, may fly for several kilometres. Males are more usually found near the swamps. In the laboratory, at 25–30°C., females of *M. uniformis* have survived to lay six egg-masses (Bertram & Samarawickrema, 1958) and under similar conditions females of *M. africana* have survived to lay four egg-masses. Survival of mated and unmated females of *M. africana* fed regularly on blood but no sugar, and kept over *Salvinia* floating in oviposition jars, is shown in fig. 2. In the mosquito cages the maximum length of life of females of *M. africana* fed on blood and sugar, and of males, fed on sugar, has been 30 and 21 days, respectively, although females of *M. uniformis* fed on blood and sugar may live for as long as 40 days (Samarawickrema, 1959). Both species are very

sensitive to low humidities and most males and unfed females are dead after exposure, over sulphuric acid and sodium hydroxide solutions, to 70 per cent. R.H. for 24 hours at a temperature of 27–29°C. As the eggs are not resistant to desiccation, it is difficult to account for the survival of both species in some parts of their range, such as the Gambia, where the fresh-water breeding places dry up during the dry season.

Eggs and hatching.

At 27–29°C., the time for development of the larva up to hatching of the egg is 6–7 days in *M. africana* and 5–6 days in *M. uniformis*. At 24°C., the

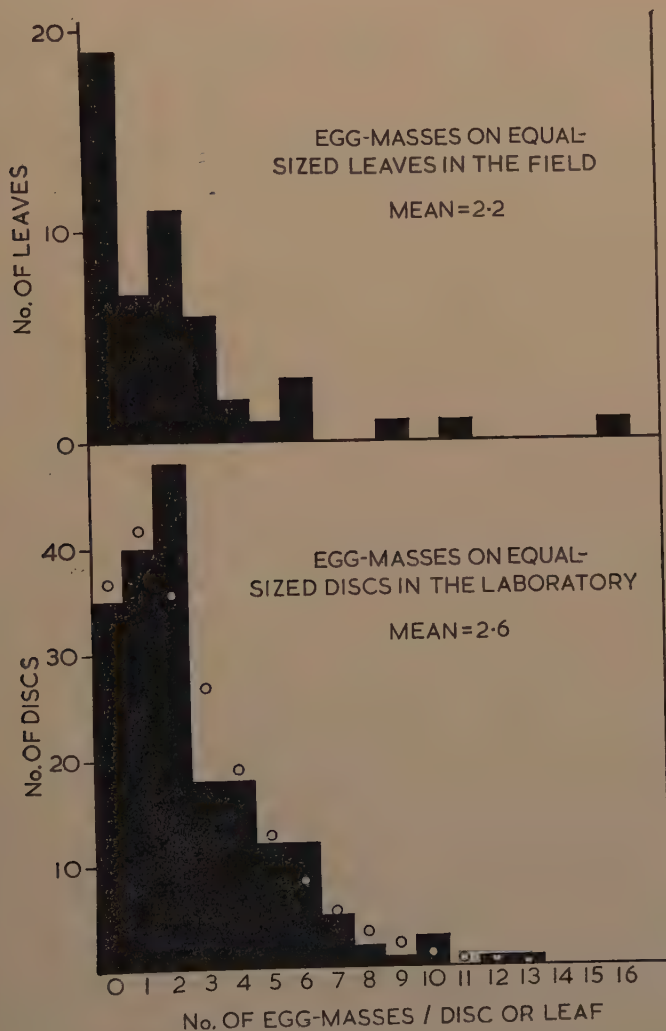


Fig. 5.—Distribution of egg-masses of *M. uniformis* laid on equal-sized discs of paper in the laboratory compared with the theoretical (binomial) distribution (o-o), and the distribution of egg-masses of both species on leaves of *Nymphaea micrantha* found in the field in the Gambia, West Africa.

duration of the egg stage is prolonged by one day. Drying the egg-masses at all stages of development of the larvae inside has not initiated diapause and egg-masses dried for more than two hours over calcium chloride have not hatched. The embryonic development of both species in the egg is a gradual and continuous process. At 27–29°C., the embryo is segmented but is still with external yolk (corresponding to Telford's (1957) 60-hr. stage in *Aedes*) at about 40 hr. in *M. uniformis* and at about 64 hr. in *M. africana*. The eggs do not withstand a temperature of 38°C. for from 24 to 32 hr. and, although some of these eggs may hatch, the larvae die during, or soon after, hatching. Many of the larvae are incompletely developed within the egg and the posterior end, particularly the siphon, is incomplete. Larvae have hatched, and developed normally, from eggs exposed to 38°C. for less than 24 hours.

Approximately 100 larvae (*M. africana*: mean no. of larvae = 111.2, range 43–170; *M. uniformis*: mean no. of larvae = 101.3, range 54–163) hatch from a normal-sized egg-mass. There were no statistically significant differences in the number of larvae hatching from first, second and third egg-masses laid by females of *M. africana* isolated from males after the first blood-meal (first egg-mass: mean no. of larvae = 120 ± 8.8 ; second egg-mass: 98 ± 6.4 ; third egg-mass: 78 ± 16.0). One insemination, therefore, is sufficient for normal fertilisation of at least three egg-masses per female. Recently, Samarawickrema (1959) has shown that in females of *M. uniformis* more ovarioles are in a resting condition in the older females.

In the laboratory, most of the larvae hatch overnight (1900 to 1000 hr.). Egg-masses kept under observation hourly through the night began to hatch one hour after sunset (2200 hr.) and continued to hatch until two hours before sunrise (0600 hr.). Attempts to alter the hatching rhythm by placing the eggs in the dark just before they were due to hatch, or placing the eggs in continuous darkness during development, have not been successful and the larvae subjected to these experiments have hatched on the same night as the controls kept in normal light and darkness.

When the larvae hatch, the tapering micropyle end of the egg is cut off and the larvae emerge into the water beneath the leaf. The newly emerged larvae do not expand their head capsules until at least one hour after emergence, and some larvae have not expanded 12 hours after hatching.

Attachment of the larvae and pupae.

The newly hatched larvae swim actively in the water and are able to respire at the surface film. McNeel (1932) concluded from observations on the newly hatched larvae of *M. perturbans* (Wlk.) that the first-instar larvae of *Mansonia*, unlike the subsequent instars, do not attach themselves to plants but respire in the same way as other mosquito larvae at the surface, and this view has also been put forward by van den Assem (1958). These authors have probably been influenced by the difference in structure in the siphon of the first-instar larva, compared with the subsequent instars, and also by the behaviour of the larvae in clean water. Numerous observations on the newly hatched larvae of both *M. africana* and *M. uniformis* have shown that the larvae will not normally attach to plants unless food, in the form of bacteria and yeasts, is also present in the water. When numerous bacteria and other food are present the first-instar larvae then readily attach to plants, brown paper, plastic foam or cork placed in the water. Carter (1950) observed the larvae of *M. uniformis* attaching themselves to grass leaves floating at the surface, and any easily penetrated surface containing air may be used for respiration.

The siphon of the first-instar larva differs from that of the later instars by the absence of the saw-like median plate (Wesenberg-Lund, 1918) conspicuous in the siphon of the other instars. The movements used by the first-instar

larvae when they are trying to attach themselves are very similar to those used by the later instars and these have already been described by Wesenberg-Lund (1918) and Edwards (1919). During these movements, the larva may hang on by the hooks on the outer tube of the siphon whilst the teeth on the inner tube are exerted by contraction of the powerful muscles attached between the inner wall of the siphon and the siphonal (axial) rod (Ingram & Macfie 1917; Wesenberg-Lund, 1918). Once the siphon is inserted in the plant, or other air-containing tissue, the teeth on the inner tube of the siphon are fully exerted and the larvae are then quite difficult to pull off. The larvae will attempt to attach themselves to any surface in the water and it is not uncommon to see them attempting to pierce the sides of a glass vessel containing them. Unlike the larvae of *M. (Coquilleltidia) richiardi* (Fic.), which are commonly found attached to plants and paper beneath the mud in the larval rearing bowls, the larvae of *Mansonioides* are found attached to plants and papers above the mud level in open water, and are seldom found beneath the mud and debris at the bottom of the rearing vessels.

Van den Assem & Metselaar (1958) experimented with *Pistia* and other plants in New Guinea and showed that there was no specific attraction of larvae to *Pistia*, the classical host plant. When the larvae of *M. africana* and *M. uniformis* are given a choice between species of plants or plants and brown paper, the final result has depended more on the survival of the plants in the culture media used than on any selection of particular species for attachment (Laurence & Smith, 1958). Some aquatic plants, such as *Myriophyllum*, *Elodea* and *Lemna trisulca*, although they may contain abundant air spaces, are unsuitable, as the plants have a thick epidermis and there are few roots. Other plants, such as *Limnobium*, *Vallisneria*, *Hygrophila*, *Utricularia* and *Lemna minor* are suitable for development but the plants have deteriorated quickly under laboratory conditions. The most successful plants used for rearing the larvae were those that lived for some time in the various culture infusions and which also possessed an abundant root supply. The young roots of plants generally are preferred, but the larvae have developed equally well on the woody roots of *Juncus* and *Carex*, the shoots of oat seedlings, and the leaves of *Limnobium*, *Salvinia* and various terrestrial grasses—and also on various types of paper. Once attached, the larva does not normally move its position unless the air supply fails. If the larva is disturbed it will make sideways movements, as though maintaining a territory against other larvae, but the larvae do not readily detach themselves. Van den Assem (1958) found that the habit of attaching themselves to plants gave larvae of *Mansonia uniformis* and *M. bonnewepsterae* Assem a survival advantage over larvae of *Culex* when the larvae and their predators were placed in small containers.

In the absence of plants and other surfaces for attachment, all the larval instars of *M. africana* and *M. uniformis* are able to respire at the surface in tap water but are unable to moult into the next instar. Normally, at the moult, the old larval skeleton is left behind attached to the host-plant and the newly moulted larva then seeks a new place for reattachment. First-instar larvae live in tap water, respiring at the surface, for 24 hours (86–92% survival of both species at 28°C.) but few larvae live for 48 hours and none have survived for 72 hours. The later instars also do not live for long in tap water in the absence of plants, and larvae about to moult die during the process of moulting. Fourth-instar larvae of *M. africana* are able to survive in tap water for 24 hours (80–87% survival at 28°C.) but larvae near pupation died whilst trying to pupate or at the pupal stage. Galliard (1939), however, was able to rear larvae of *M. indiana* Edw. to the adult stage in clear water and with no vegetation. The larvae of *M. africana* and *M. uniformis* live for longer periods in the absence of plants if food infusion is added to the water, but they then gain additional support from the bacterial film formed at the surface. First-instar larvae have lived in

guineapig-faeces infusion for 10 days, respiring at the surface, and some of these larvae moulted successfully. Fourth-instar larvae have lived for 48 hours in guineapig-faeces infusion in the absence of plants and paper, but readily attached themselves and pupated when paper was added. The larvae may survive for short periods without plants but it is unlikely that the complete life-cycle is possible under these conditions.

The structure of the siphon in the larvae of *M. africana* and *M. uniformis* is the same; the only difference in the posterior end of the larva, and indeed the only difference of morphology between the larvae of the two species, is the presence of more numerous, shorter branches in the hair tuft B, lying between the siphon and the anal segment, in *M. africana* (fig. 7).

The pupae of *Mansonia* also use the submerged parts of aquatic plants for their air supply and, in the laboratory, pupation and pupal development to adult

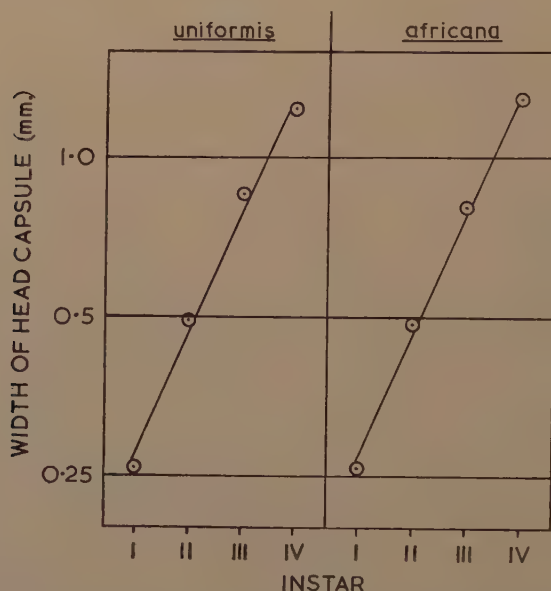


Fig. 6.—Width of head capsules (mean head width of 25 larvae of each instar) of *M. africana* and *M. uniformis*.

have been obtained on a variety of plants, such as *Pistia*, *Salvinia* and various Gramineae, *Phalaris*, *Carex*, *Glyceria*, *Juncus*, *Phleum*, *Dactylis* and *Avena*, as well as paper (Laurence & Smith, 1958). The pupae may be attached to the roots or, less commonly, to the leaves of the plants. Normally the pupa does not detach itself until just before emergence and, once detached, cannot reattach itself. If the pupae are removed from the plant or paper they float at the surface, although without float hairs, and some of the pupae can complete development although removed within 24 hours of pupation. In *M. africana*, 22 per cent. (2–51%) of 144 pupae removed within 24 hours completed development, compared with 14 per cent. (4–25%) of 118 removed within 48 hours and 43% (28–70%) of 135 removed within 72 hours and ready to detach themselves normally. Fresh pupae, which have been dislodged during pupation, are unable to develop at the surface and soon sink and die.

The pupal respiratory horns of *M. africana* are longer than those of *M. uniformis*, and the bifurcations of the male genitalia of the pupa are widened apically, whereas in *M. uniformis* these bifurcations are close together. No other differences have been found between the pupae of the two species.

Moulting and length of life-cycle, metabolism.

At 25–30°C., the larvae of both species of *Mansonioides* moult at intervals of five or more days and the first adults appear 21–31 days from the hatching

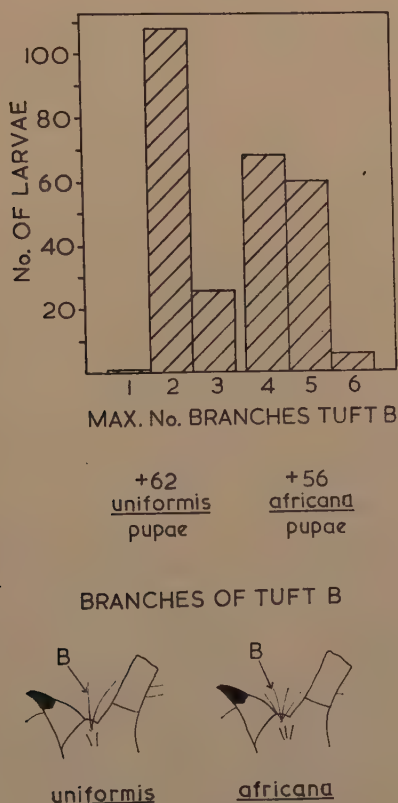


Fig. 7.—Result of rearing equal numbers of newly hatched larvae of *M. africana* and *M. uniformis* together. The fourth-stage larvae are separated only by the number of branches of tuft B, and this is illustrated below.

of the eggs (fig. 9). At 18–24°C., the third and fourth larval instars moulted after approximately 12 days, the total period from second-stage larva to adult mosquito being 40 days. At the moult from one larval instar to another the old larval skin is left attached to the plant, and the newly moulted larva has to reattach itself at another point. If the larva becomes detached during moulting it then is unable to get rid of the old larval skin and dies. At the moult from the last larval instar into the pupa the abdomen of the pupa remains within the

larval skin until the pupal respiratory horns are firmly embedded into the plant, usually near the point of attachment of the larva. Once attached by the thoracic respiratory horns, the pupa then throws off the old larval skin by violent movements of the abdomen. The process of pupation is the same in both species of *Mansonioides* and resembles that described by Galliard (1934) for *Mansonia richiardi*.

One of the striking features of the biology of *M. africana* and *M. uniformis* is the close similarity in the growth of the larvae of the two species. The size of the four larval instars is the same (fig. 6) and, if equal numbers of newly hatched larvae of both species are reared together in the same culture infusion, the larvae grow at the same rate and begin to pupate about the same time. The results of four experiments of rearing equal numbers of first-instar larvae together are shown in fig. 7. The larvae were reared up to the emergence of the first adult; the pupae were then separated by examination of the pupal horns and male genitalia, and the larvae were separated by counting the number of branches on tuft B on both sides of the abdomen (fig. 7). A total of 56 pupae and 134 fourth-stage larvae (with 4-6 branches in tuft B) of *M. africana* and 62 pupae and 135 fourth-stage larvae (with 1-3 branches in tuft B) of *M. uniformis* were obtained in four experiments by rearing together 340 first-instar larvae of each species hatched on the same day. There is therefore no evidence from these mixed cultures that one species is able to develop more rapidly and, with this advantage, replace the other species by competition. If, however, the results from a large number of routine rearing bowls are compared and, for the comparison, the period in days from the hatching of the eggs to the emergence of the first adult is taken to represent the relative speed of development, then *M. uniformis* tends to develop more quickly than *M. africana* (fig. 9). The mean period from hatching of eggs to the first adult emergence was 24.3 days in *M. uniformis* and 25.5 days in *M. africana*. Although the two species in these routine cultures were reared in different but adjacent insectaries, the temperature variation was the same in both of them; for *M. africana*: average weekly minimum temperature 27.0°C. (range 25-29°C.), average weekly maximum temperature 29.4°C. (range 27-33°C.); for *M. uniformis*: average weekly minimum temperature 27.0°C. (range 26-29°C.), average weekly maximum temperature 29.5°C. (range 28-33°C.). There is, therefore, some evidence that the larvae of *M. uniformis* develop slightly faster than those of *M. africana*. Associated with this, indicating a difference between the larvae in metabolism, may be the slightly greater resistance of the larvae of *M. uniformis* to temperatures above 35°C., although larvae of both species are killed when exposed for one hour at 40.5°C. in tap water. Exposure of the fourth-instar larvae of both species, kept previously at 27-29°C., to constant temperatures of from 40 to 46°C., controlled thermostatically in a water bath, showed that, at all exposure times, when the larvae of *M. africana* were killed or in heat coma, some larvae of *M. uniformis* were alive and active (fig. 8). Experiments with newly hatched first-instar larvae placed in an incubator at 38°C. also demonstrated a greater resistance of *M. uniformis* to high temperatures (Table IV).

Although there may be slight differences in larval metabolism, there are no observable differences in the feeding behaviour and in the structure of the mouthparts of the larvae of the two species. The two species have been reared with equal success in the various culture infusions used in the laboratory (Laurence & Smith, 1958). The larvae feed only when attached by their siphons, either to plants and other surfaces, or to the surface film. During feeding, water is drawn towards the body by movements of the mouthbrushes and the inner brushes are combed at each inward movement by the mandibles (Wesenberg-Lund, 1918). The larvae are filter feeders only and are able to filter suspended materials very quickly from the water. Food is passed back through the oesophagus regularly

at 25°C. at about 15-second intervals. The first-instar larvae take in from the culture infusion small particles the size of bacteria, yeast cells and small flagellates. They will also accumulate indian-ink particles quickly in the oesophagus and these particles (less than 2μ in diameter) are also taken in by the second.

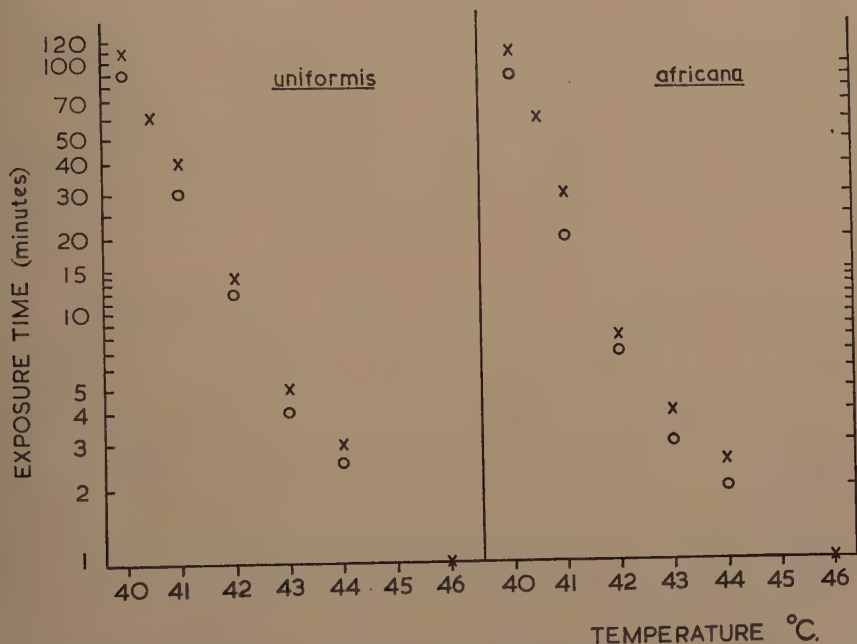


Fig. 8.—Thermal death points for fourth-instar larvae of *M. africana* and *M. uniformis*. x, all larvae dead or in heat coma; o, some larvae alive and recovered.

third and fourth instars. The later instars are able to feed on larger-sized particles. Second-stage larvae are able to pull rotifers and large protozoa into the vicinity of the mouth but the largest particles in the gut are about 20μ long. Third-stage larvae will take in large flagellates, such as *Phacus*, and small rotifers about 50μ across, and fourth-stage larvae may take in plant debris up to 200μ long.

TABLE IV.

Percentage survival after 24 hours in tap water at 27–29°C. of first-instar larvae previously exposed to 38°C. for 0–6 hours.

			Exposure time (hours)						
			0	1	2	3	4	5	6
<i>M. africana</i>	86	73	60	47	40	24	22
<i>M. uniformis</i>	92	82	81	73	53	55	48

One hundred or more larvae used in four or more replicate experiments at each exposure time.

Not all the material swept up to the mouth is taken in, and the first-instar larvae produce a long thread from between the maxillae in which are bound rejected particles from the mouthparts. This thread may extend back to the eighth abdominal segment before breaking away and may be formed at the rate of 1 mm. every 20 seconds. The long thread of rejected particles is not so marked in the later instars although the rejected particles may be bound together as they issue from between the maxillae. Larvae of both species collected from the same breeding place in the Gambia had been feeding on a variety of Chrysophyceae, the cysts of which were mixed with smaller particles in the gut. The feeding position taken up by the larvae is very variable; some larvae may be attached with the body horizontal, others with the head upwards or with the head downwards. In all these positions the larvae are capable of sweeping water in towards the head from distances greater than the length of their bodies.

If the larvae are very crowded, development may be delayed and the length

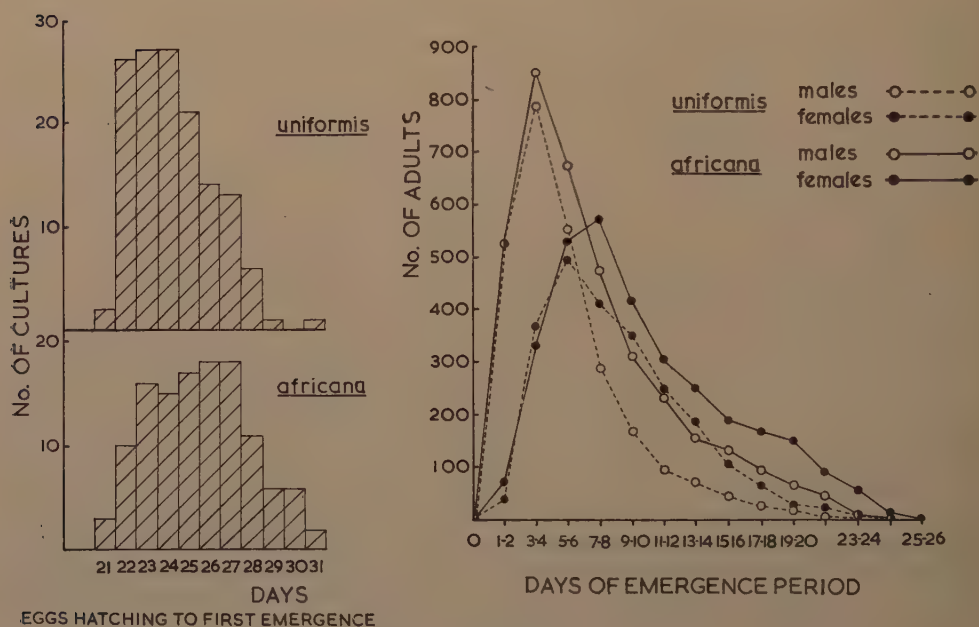


Fig. 9.—Duration of development, from hatching of eggs to first emergence of adults, at 27–29.5°C., of various cultures of *M. africana* and *M. uniformis*, and the pattern of emergence during the emergence period of each species.

of the life-cycle may be doubled. Two cultures of *M. africana* set up on the same day, one with 300 larvae and one with over 600 larvae, produced the first adults 24 and 41 days later, respectively. In the crowded culture, second-stage larvae were still present 22 days after hatching. When numerous larvae are present, the emergence period of the adult mosquitos is also prolonged, suggesting that in crowded cultures pupation of some of the larvae is delayed.

Emergence of the adult.

The pupal period in both *M. africana* and *M. uniformis* at 25–30°C. is from three to four days. Male larvae develop more rapidly than female and there is a preponderance of male pupae in the early period of pupation. There is a

corresponding peak of emergence of male adults three to four days after the onset of emergence, which is followed by the main emergence of the females (fig. 9). The pattern of emergence is the same in both species. The pupae detach themselves normally within 12 hours of emergence and then float at the surface. The actual time taken to emerge, from air becoming first visible inside the pupal skin to the adult resting on the surface, is from 15 to 20 minutes. Once emerged, the adult mosquito may rest on the surface for 20 to 30 minutes. Over a period of 24 hours, adult mosquitos of both species emerged from pupae in every hour, but more adults emerged in the five-hour period from 1700 to 2200 hr. than in other five-hour periods. The impression obtained from routine rearing was that the main emergence of the mosquitos was overnight. There is thus no well-defined period of emergence, different in the two species, which might act as a mating barrier between them.

Discussion.

There is no evidence at present why *M. uniformis* should be a widely distributed species, yet *M. africana* is confined to the continent of Africa. The geographical distribution of the two species suggests that *M. africana* may have evolved in isolation in Africa (Mattingly & Brown, 1955), and there is some evidence of present-day speciation in *M. uniformis* in that strains from Malaya and Ceylon are partially infertile with the strain from Africa. A close comparison of the two species has shown that differences in biology between them are very small. It is unlikely that the two species are the result of ecological speciation. In Africa, both species are sufficiently abundant for them to be both described as very successful. Both species are common throughout most of tropical Africa, although *M. uniformis* is apparently less common west of longitude 10°E. There is no evidence at present that *M. uniformis*, which would appear to be a more recent inhabitant, is extending its range at the expense of, and in competition with, *M. africana*.

In the field, both species of *Mansonioides* are found living side by side, although there may be differences in habitat range, such as those described by Haddow (1945) in Uganda, where *M. africana* may be widely distributed and *M. uniformis* more abundant in open country. How this can be related to the laboratory observations is a matter of speculation. The females of *M. uniformis* show a greater visual sensitivity at oviposition and this may also be responsible for the greater activity shown by this species overnight after a blood-meal. *M. africana* is more sensitive to organic pollution of water and there is thus some evidence that the two species may choose different types of breeding place (as suggested by Hopkins, 1952), although both species can be found breeding together. The breeding place, which in *Mansonioides* is a complex of floating leaves surrounded by vegetation with easily penetrated aerenchyma, is selected by the female mosquito and a difference in the biology here, at oviposition, may profoundly affect the distribution of the species. In some parts of India, rural filariasis, transmitted by *M. annulifera*, is an occupational disease of villages where coconut husks are soaked in water pits, thus providing breeding places for this species which is attracted to water polluted with organic material (Iyengar, 1938).

In the biology of the early stages of the life-history, there is a surprising lack of differentiation between the two species, although there are indications of differences in the metabolism of the egg and larva. The lack of biological differentiation is paralleled by the absence of distinct morphological characters which differentiate the early stages. The larvae live in a more stable environment than the adult mosquitos and also live in a more stable environment than other mosquito larvae. Although the aerenchymatous tissue of plants may be rich

in oxygen (Sifton, 1945), this does not seem to be a specific requirement of these root-piercing larvae, as they can be found attached to air spaces in decayed vegetation, to air spaces in peat, and also develop readily when attached to paper, taking their oxygen from the air spaces compressed between the paper fibres. Attachment to plants for respiration means loss of mobility and, in fact, once the larvae are attached they move very little, but attachment also provides protection from predators (van den Assem, 1958). The siphon of the larva is complex but a similar root-piercing habit has been evolved in other mosquito species in the genus *Ficalbia* (Mattingly & Grjebine, 1958). The origin of the root-piercing habit is shown by the larvae of some species of *Culex* and *Ficalbia* which attach themselves to bubbles of air on plants below the surface of the water (Hopkins, 1952). What is striking is that two mechanisms have been evolved, both in *Mansonia* and in *Ficalbia*—one in the larva and one in the pupa. The method of fixation of the pupa depends upon the prior attachment of the last larval skin and, consequently, the root-piercing habit of the pupa must have evolved later than the root-piercing habit of the larva. But the evolution of the two mechanisms in the life-history, which ensures the attachment of both larva and pupa, indicates the survival advantage to the insect of the habit of piercing aquatic plants to obtain oxygen.

Summary.

The distribution and biology of two related species of mosquito, *Mansonia* (*Mansonioides*) *africana* (Theo.) and *M. (M.) uniformis* (Theo.), have been compared. *M. uniformis* is found from China to Africa, whereas *M. africana* is restricted to the continent of Africa. The two species do not interbreed although mating, but no insemination, is possible in the laboratory. Strains of *M. uniformis* from Africa, Ceylon and Malaya are interfertile, but crosses between the African and the other strains, especially, showed a reduction in fertility of the eggs produced and thus some evidence of speciation.

The two species show the same adult behaviour at mating, feeding (both in the field and in the laboratory) and during oviposition. Both species are stenogamous and mate readily in small cages. The first blood-meal is taken approximately 24 hours after emergence and immediately after each oviposition, 3–5 days after the previous blood-meal. *M. uniformis* is more active directly after the blood-meal.

The gravid females will lay their eggs on the undersides of most surfaces floating on the water, such as leaves, cork and paper discs. The females prefer to lay on leaves floating with the underside meeting the surface of the water at an angle rather than on leaves floating flat on the surface. The two species differ, in the laboratory, in the responses of the gravid females to water pollution and to the background of the breeding site. Females of *M. africana* are more sensitive to pollution by organic material, and females of *M. uniformis* under laboratory conditions show a greater visual sensitivity.

The length of adult life of females in the laboratory has been up to 30 days in *M. africana* but *M. uniformis* has lived for up to 40 days. Both species are sensitive to low humidities and most males and unfed females do not survive 70 per cent. R.H. for 24 hours at 27–29°C.

The biology of the early stages of the life-history is almost identical in the two species although development is slightly faster in *M. uniformis*. At 27–29°C., the larvae of *M. uniformis* develop more quickly in the egg and hatch after five–six days, 24 hours before the larvae of *M. africana*. There is evidence that the period from hatching to emergence of the first adult is also faster in *M. uniformis*, with a mean of 24.3 days compared with 25.5 days in *M. africana*, although larvae reared together may emerge at the same time and in equal numbers.

The larvae also differ in their resistance to high temperatures, and above 40°C. some larvae of *M. uniformis* survive at exposure times lethal for *M. africana*.

The larvae of both species are filter feeders and feed on the same type of food. They will attach themselves readily to most plants and other surfaces containing air, such as paper, placed in the water, provided that food in the form of bacteria, yeasts and other organisms is also present. Any air store that can be penetrated by the larval siphon is used, and there is no selection of any particular plant species for attachment. The larvae are able to survive in tap water, respiring at the surface, for 24 hours but usually cannot live under these conditions for 48 hours. If food is present the larvae may live for longer, attached to the bacterial film at the surface of the water, but most larvae die under these conditions while moulting.

The pupae are able to develop attached to plants or to paper. Before emergence, about three days after pupation, the pupae detach themselves and then float at the surface. If the incompletely developed pupae are detached one or two days before emergence, up to 51 per cent. of the pupae can develop normally at the surface. The pattern of emergence is the same in *M. africana* and *M. uniformis*. The habit of attaching themselves to plants for respiration in the larval and pupal stages provides protection and a more stable environment for the early stages.

The implications of the similarity in the biology of the two species are discussed with reference to possible competition between the two species in Africa. It is concluded that *M. africana* has evolved in isolation in Africa and that *M. uniformis* is most probably a more recent invader. Differences in the behaviour of the female mosquito in the selection of the breeding place may determine the local distribution of the two species and there is some evidence that the habitat ranges of the two species do not completely coincide.

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References.

- ANTONIPULLE, P., DAVID, H. V. & KARUNARATNE, M. D. R. (1958). Biology and control of *Taeniorhynchus (Mansonioides) uniformis* Theobald, the chief vector of rural filariasis in Ceylon.—*Bull. World Hlth Org.* **19** pp. 285–295.
- VAN DEN ASSEM, J. (1958). Some experimental evidence for the survival value of the rootpiercing habits of *Mansonia* larvae (Culicidae) to predators.—*Ent. exp. appl.* **1** pp. 125–129.
- VAN DEN ASSEM, J. & METSELAAR, D. (1958). Host-plants and breeding places of *Mansonia (Mansonioides) uniformis* in Netherlands New-Guinea.—*Trop. geogr. Med.* **10** pp. 51–55.

- BEEUWKES, H., KERR, J. A., WEATHERSBEE, A. A. & TAYLOR, A. W. (1933). Observations on the bionomics and comparative prevalence of the vectors of yellow fever and other domestic mosquitoes of West Africa, and the epidemiological significance of seasonal variations.—*Trans. R. Soc. trop. Med. Hyg.* **26** pp. 425–447.
- BERTRAM, D. S. & SAMARAWICKREMA, W. A. (1958). Age determination for individual *Mansonioides* mosquitoes.—*Nature, Lond.* **182** pp. 444–446.
- BONNE-WEPSTER, J. & BRUG, S. L. (1939). Observations on the breeding habits of the subgenus *Mansonioides* (Genus *Mansonia*, Culicidae).—*Tijdschr. Ent.* **82** pp. 81–90.
- BRUG, S. L. & DE ROOK, H. (1930). Filariasis in Ned.-Indië. II. De overbrenging van *Filaria malayi*.—*Geneesk. Tijdschr. Ned.-Ind.* **70** pp. 451–474.
- BRYGOO, E. R. (1957). La filariose humaine à Madagascar.—*Arch. Inst. Pasteur Madagascar* **26** pp. 23–39.
- BUCKLEY, J. J. C. & EDESON, J. F. B. (1956). On the adult morphology of *Wuchereria* sp. (*malayi*?) from a monkey (*Macaca irus*) and from cats in Malaya, and on *Wuchereria pahangi* n. sp. from a dog and a cat.—*J. Helminth.* **30** pp. 1–20.
- BUCKLEY, J. J. C., NELSON, G. S. & HEISCH, R. B. (1958). On *Wuchereria patee* n. sp. from the lymphatics of cats, dogs and genet cats on Pate Island, Kenya.—*J. Helminth.* **32** pp. 73–80.
- CARTER, H. F. (1950). The genus *Taeniorhynchus* Lynch Arribalzaga (Diptera, Culicidae) with special reference to the bionomics and relation to disease of the species occurring in Ceylon.—*Ceylon J. Sci. (B)* **24** pp. 1–26.
- DAUBNEY, R. & HUDSON, J. R. (1933). Rift Valley fever.—*E. Afr. med. J.* **10** pp. 2–19.
- VAN DIJK, W. J. O. M. (1958). Transmission of *Wuchereria bancrofti* in Netherlands New-Guinea.—*Trop. geogr. Med.* **10** pp. 21–33.
- EDWARDS, F. W. (1919). The larva and pupa of *Taeniorhynchus richiardii*, Fic. (Diptera Culicidae).—*Ent. mon. Mag.* **55** pp. 83–88.
- FENG (Lan-chou) (1938). A critical review of literature regarding the records of mosquitoes from China. Parts I–II.—*Peking nat. Hist. Bull.* **12** pp. 169–181, 285–318.
- GALLIARD, H. (1934). Notes sur la biologie et l'anatomie de la larve de *Taeniorhynchus richiardii* Ficalbi.—*Ann. Parasit. hum. comp.* **12** pp. 465–471.
- GALLIARD, H. (1939). Sur la biologie des culicidés du genre *Mansonia* R. Blanchard en Indochine.—*Ann. Parasit. hum. comp.* **17** pp. 177–186.
- GÂNDARA, Á. F. (1956). Subsídio para o estudo dos “Culicidae” (Diptera) de Angola.—*An. Inst. med. trop.* **13** pp. 387–418.
- GILLET, J. D. (1957). Age analysis in the biting-cycle of the mosquito *Taeniorhynchus* (*Mansonioides*) *africanus* Theobald, based on the presence of parasitic mites.—*Ann. trop. Med. Parasit.* **51** pp. 151–158.
- GUNewardENE, K. (1956). Observations on the development of *Dirofilaria repens* in *Aedes* (*Stegomyia*) *albopictus* and other common mosquitoes of Ceylon.—*Ceylon J. med. Sci.* **9** pp. 45–53.
- HADAWAY, A. B. (1950). Observations on mosquito behaviour in native huts.—*Bull. ent. Res.* **41** pp. 63–78.
- HADDOW, A. J. (1942). The mosquito fauna and climate of native huts at Kisumu, Kenya.—*Bull. ent. Res.* **33** pp. 91–142.

- HADDOW, A. J. (1945). The mosquitoes of Bwamba County, Uganda. II. Biting activity with special reference to the influence of microclimate.—*Bull. ent. Res.* **36** pp. 33–73.
- HADDOW, A. J. (1954). Studies of the biting-habits of African mosquitos. An appraisal of methods employed, with special reference to the twenty-four-hour catch.—*Bull. ent. Res.* **45** pp. 199–242.
- HADDOW, A. J. & DICK, G. W. A. (1948). Catches of biting Diptera in Uganda, with anaesthetized monkeys as bait.—*Ann. trop. Med. Parasit.* **42** pp. 271–277.
- HADDOW, A. J. & GILLETT, J. D. (1958). Laboratory observations on the oviposition-cycle in the mosquito *Taeniorhynchus* (*Coquillettidia*) *fusco-pennatus* Theobald.—*Ann. trop. Med. Parasit.* **52** pp. 320–325.
- HADDOW, A. J., GILLETT, J. D. & HIGHTON, R. B. (1947). The mosquitoes of Bwamba County, Uganda. V. The vertical distribution and biting-cycle of mosquitoes in rain-forest, with further observations on microclimate.—*Bull. ent. Res.* **37** pp. 301–330.
- HOPKINS, G. H. E. (1952). Mosquitoes of the Ethiopian Region. I. Larval bionomics of mosquitoes and taxonomy of Culicine larvae.—2nd edn., 355 pp. London, Brit Mus. (Nat. Hist.).
- HOWITT, B. F., DODGE, H. R., BISHOP, L. K. & GORRIE, R. H. (1949). Recovery of the virus of eastern equine encephalomyelitis from mosquitoes (*Mansonia perturbans*) collected in Georgia.—*Science* **110** pp. 141–142.
- INGRAM, A. & MACFIE, J. W. S. (1917). The early stages of certain West African mosquitos.—*Bull. ent. Res.* **8** pp. 135–154.
- IYENGAR, M. O. T. (1935). Biology of Indian mosquito larvae that attach themselves to the roots of water plants.—*Proc. R. ent. Soc. Lond.* **10** pp. 9–11.
- IYENGAR, M. O. T. (1938). Studies on the epidemiology of filariasis in Travancore.—*Indian med. Res. Mem.* no. 30, 179 pp.
- JAYEWICKREME, S. H. (1953). Nocturnal mating in *Taeniorhynchus* (*Mansonioides*) *uniformis* (Theobald).—*Nature, Lond.* **171** p. 577.
- JAYEWICKREME, S. H. & NILES, W. J. (1952). A technique for rearing *Mansonioides* larvae in the laboratory.—*Ceylon J. Sci. (B)* **25** pp. 1–6.
- KERR, J. A. (1933). Studies on the abundance, distribution and feeding habits of some West African mosquitos.—*Bull. ent. Res.* **24** pp. 493–510.
- KOKERNOT, R. H., SMITHBURN, K. C., MUSPRATT, J. & HODGSON, B. (1957). Studies on arthropod-borne viruses of Tongaland. VIII. Spondweni virus, an agent previously unknown, isolated from *Taeniorhynchus* (*Mansonioides*) *uniformis* Theo.—*S. Afr. J. med. Sci.* **22** pp. 103–112.
- LAURENCE, B. R. (1959). Oviposition by *Mansonioides* mosquitoes in the Gambia, West Africa.—*Proc. R. ent. Soc. Lond. (A)* **34** pp. 161–170.
- LAURENCE, B. R. & SMITH, S. A. (1958). The breeding of *Taeniorhynchus* (subgenus *Mansonioides*) mosquitoes in the laboratory.—*Trans. R. Soc. trop. Med. Hyg.* **52** pp. 518–526.
- LAVOPIERRE, M. M. J. (1958). Presence of a factor inhibiting biting in *Aedes aegypti*.—*Nature, Lond.* **182** pp. 1567–1568.
- LEWIS, D. J. (1945). Observations on the distribution and taxonomy of Culicidae (Diptera) in the Sudan.—*Trans. R. ent. Soc. Lond.* **95** pp. 1–24.

- LEWIS, D. J. (1947). General observations on mosquitos in relation to yellow fever in the Anglo-Egyptian Sudan.—*Bull. ent. Res.* **37** pp. 543–566.
- MACFIE, J. W. S. & INGRAM, A. (1916). The domestic mosquitos of Accra.—*Bull. ent. Res.* **7** pp. 161–177.
- MCNEEL, T. E. (1932). Observations on the biology of *Mansonia perturbans* (Walk.).—*Proc. N.J. Mosq. Ext. Ass.* **19** pp. 91–96.
- MATTINGLY, P. F. (1949). Studies on West African forest mosquitos. Parts I–II.—*Bull. ent. Res.* **40** pp. 149–168, 387–402.
- MATTINGLY, P. F. (1957). Notes on the taxonomy and bionomics of certain filariasis vectors.—*Bull. World Hlth Org.* **16** pp. 686–696.
- MATTINGLY, P. F. & BROWN, E. S. (1955). The mosquitos (Diptera: Culicidae) of the Seychelles.—*Bull. ent. Res.* **46** pp. 69–110.
- MATTINGLY, P. F. & GRJEBINE, A. (1958). Révision du genre *Ficalbia* Theobald et discussion de la position systématique des *Ravenalites* Doucet (Diptera, Culicidae).—*Mém. Inst. sci. Madagascar* (E) **9** pp. 259–290.
- PHILIP, C. B. (1930). Studies on transmission of experimental yellow fever by mosquitos other than *Aedes*.—*Amer. J. trop. Med.* **10** pp. 1–16.
- PHILIP, C. B. (1931). List of mosquitos collected in Nigeria, West Africa, incidental to research on yellow fever.—*Proc. ent. Soc. Wash.* **32** pp. 44–47.
- DE ROOK, H. (1957). Report of an investigation on filariasis in the Berau Region (Inanwatan District, north-west New Guinea).—*Tech. Pap. S. Pacif. Comm.* no. 105, 19 pp.
- SAMARAWICKREMA, W. A. (1959). Laboratory studies on the biology of *Taeniorhynchus* (*Mansonioides*) *uniformis* (Theobald) and *T. (M.) annulifera* (Theobald) from Ceylon.—Unpublished Ph.D. thesis, Univ. London.
- SCHWETZ, J. (1930). Contributions à l'étude de la biologie de *Taeniorhynchus* (*Mansonioides*) *africanus* et de *Taeniorhynchus* (*Coquillettidia*) *aurites* au Congo Belge.—*Rev. Zool. Bot. afr.* **18** pp. 311–329.
- SIFTON, H. B. (1945). Air-space tissue in plants.—*Bot. Rev.* **11** pp. 108–143.
- SMITH, A. (1955). The transmission of bancroftial filariasis on Ukara Island, Tanganyika. I–IV.—*Bull. ent. Res.* **46** pp. 419–444, 495–515.
- VAN SOMEREN, E. C. C., HEISCH, R. B. & FURLONG, M. (1958). Observations on the behaviour of some mosquitos of the Kenya coast.—*Bull. ent. Res.* **49** pp. 643–660.
- TATE, P. & VINCENT, M. (1936). The biology of autogenous and anautogenous races of *Culex pipiens* L. (Diptera: Culicidae).—*Parasitology* **28** pp. 115–145.
- TELFORD, A. D. (1957). The pasture *Aedes* of central and northern California. The egg stage: gross embryology and resistance to desiccation.—*Ann. ent. Soc. Amer.* **50** pp. 537–543.
- TOUMANOFF, C. (1958). Filariose humaine et sa transmission dans la Basse-Guinée (Estuaire du Rio Nunez).—*Bull. Soc. Path. exot.* **51** pp. 908–912.
- VARLEY, G. C. (1937). Aquatic insect larvae which obtain oxygen from the roots of plants.—*Proc. R. ent. Soc. Lond.* (A) **12** pp. 55–60.
- VARLEY, G. C. [1959]. [Account of specimens exhibited at meeting.]—*Proc. R. ent. Soc. Lond.* (C) **23** pp. 47–48.
- VINCKE, I. H. (1959). Note sur les culicidés dans la vallée de la Lufira (1941–1942).—*Riv. Parassit.* **20** pp. 423–434.

- WESENBERG-LUND, C. (1918). Anatomical description of the larva of *Mansonia richiardi* (Ficalbi) found in Danish freshwaters.—*Vidensk. Medd. dansk. naturh. Foren.* **69** pp. 277–328.
- WHARTON, R. H. (1957). Studies on filariasis in Malaya: notes on the breeding of *Mansonia (Mansonioides)* mosquitoes in the laboratory.—*Ann. trop. Med. Parasit.* **51** pp. 297–300.
- WHARTON, R. H. (1959a). *Dirofilaria magnilarvatum* Price, 1959 (Nematoda: Filarioidea) from *Macaca irus* Cuvier. IV. Notes on larval development in *Mansonioides* mosquitoes.—*J. Parasit.* **45** pp. 513–518.
- WHARTON, R. H. (1959b). Age determination in *Mansonioides* mosquitoes.—*Nature, Lond.* **184** Suppl. no. 11 pp. 830–831.
- WILLIAMS, M. C., WEITZ, B. & MCCLELLAND, G. A. H. (1958). Natural hosts of some species of *Taeniorhynchus* Lynch Arribalzaga (Diptera, Culicidae) collected in Uganda, as determined by the precipitin test.—*Ann. trop. Med. Parasit.* **52** pp. 186–190.

THE IDENTITY OF *PSEUDODONIELLA LAENSIS* MILLER
(HEMIPTERA, MIRIDAE), ASSOCIATED WITH CACAO
IN NEW GUINEA AND PAPUA.

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In the course of a recent preliminary revision of the MIRIDAE of the subfamily BRYOCORINAE in the British Museum (Natural History), the results of which will be reported in a paper now in preparation, the genus *Pseudodoniella* China & Carvalho was examined. The investigation revealed that the two species, *P. laensis* and *P. szentivanyi*, both described by Miller in 1957, are definitely conspecific. Because of the importance of the species as a pest of cacao in New Guinea and Papua, a short note is published here in advance in order to clarify this problem and make available a name for biological work.

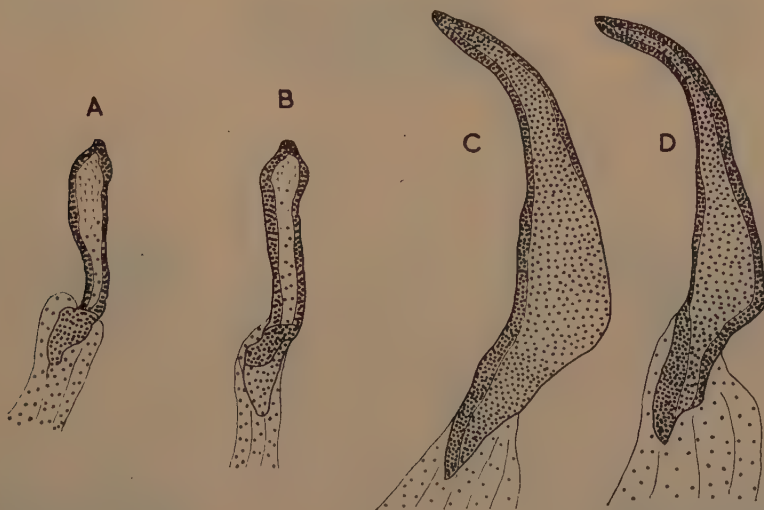


Fig. 1.—Male genitalia of *Pseudodoniella laensis*. A, B, right paramere; C, D, left paramere. (In A, C, the basal portion is flat on the microscope slide, in B, D, it is slightly tilted.)

Miller (1957) based his descriptions of the two species entirely on colour, although he provided some sketches of the head and thorax (depicting both dorsal and lateral aspects) and an outline of the right paramere. This should be taken in conjunction with the couplet in the key he constructed for the separation of *Pseudodoniella* species which distinguishes *P. laensis* ("apex of scutellum in profile broadly rounded") from *P. szentivanyi* ("apex of scutellum in profile narrowly rounded"); but this character is by no means definitive as there are intermediates. Moreover, there is an overlap in the variation of colour (fig. 2).

The structure of the head, antennae, and frontal tubercle is also identical. Finally, the writer cannot appreciate any difference in the structure of the male genitalia in Miller's two nominal species (fig. 1), and accordingly is compelled to conclude that they are identical. *P. laensis* Miller is the correct name for this species for it takes paragraph priority over *P. szentivanyi* Miller.



Fig. 2.—Pattern of dark markings on the pronotum of *Pseudodoniella laensis*. Patterns A-D and K are shown by specimens from Amele, E, F by specimens from Bubia, G, H, and J by specimens from Lae and J-M by specimens from Popondetta.

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Reference.

MILLER, N. C. E. (1957). Two new species of *Pseudodoniella* China & Carvalho (Hemiptera, Miridae).—*Bull. ent. Res.* **48** pp. 57–58.

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KILLING HOUSE-FLIES, *MUSCA DOMESTICA* L., BY MEANS OF HANGING DROPS OF INSECTICIDE.

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26.

In the practical control of adult house-flies, *Musca domestica* L., within buildings, residues of contact insecticides are produced in various ways; for example, by application of wettable powders to walls and ceilings, and by means of suspended objects, *e.g.*, cords (Kilpatrick & Schoof, 1956) or strips of cloth (Wichmand, 1953) impregnated with insecticides. A feature common to all these methods is that only very minute quantities of insecticide reach the external surfaces of the flies, and hence the insecticides used must be substances very toxic to the flies. This, in conjunction with other practical requirements, such as stability of the insecticide and avoidance of risk to man in its use, means that the choice of insecticidal substances suitable for fly control by residues is restricted.

Among other consequences, the narrow choice aggravates the difficulties of controlling resistant strains of house-fly. When one insecticide is used in a locality and flies resistant to it appear, they can often be controlled by the use of another insecticide, if suitably chosen. Control continues until a strain resistant to the second insecticide appears, when a third insecticide is used, and so on (see, for example, Keiding, 1959). However, both the restricted number of possible compounds and present methods of application hamper changes of insecticide.

If methods for practical application of residues could be introduced such that the quantity of insecticide reaching the surfaces of the flies was larger, compounds less toxic to the flies could be used, and hence the choice of insecticides would be widened; some of the insecticides now in use could be employed more effectively, but this is less important from the present point of view. If a method facilitated change of insecticide, this would be a further advantage. Indeed, if changes of insecticide could be made frequently enough, resistant strains might not appear.

This paper describes basic laboratory work on a possible method for giving house-flies relatively large doses of liquid insecticide. The principle is this: a drop of liquid of considerable size will hang (due to interfacial forces) on the lower end of a thin vertical wire; if the liquid will wet the cuticle of a fly readily, a fleeting contact of the fly with the drop may transfer a substantial volume of liquid to the surface of the fly. Thus, if the liquid is a contact insecticide, the fly may be killed. As an example of the volumes of suspensible drops, 3 μ l. of mineral oil can be hung on a wire 0.3 mm. in diameter; the diameter of a sphere of this volume would be 1.8 mm.

In the course of the work, different devices on which drops could be hung were constructed, and different methods of putting drops on them were tried; the behaviour of flies making contact with drops was observed, and the doses of liquid collected by flies were measured; the over-all efficiency of insecticidal drops was tested by giving groups of flies access to drops; and the effects of different external factors, *e.g.*, illumination, were examined. The results of the experiments were encouraging, though further development of the principle would be necessary before it found practical application.

Materials and Methods.

Unless otherwise stated, all experiments were carried out at 27°C. and 65 per cent. relative humidity.

Test insects.

The test insects were adult house-flies of a normal laboratory (insecticide-susceptible) strain. They were reared at 27°C. and 70 per cent. R.H., and the breeding technique was essentially that used by Parkin & Green (1957). Before exposure to insecticide the flies were fed with 35 per cent. v/v milk in tap-water, supplied on cotton-wool pads, and after exposure with 50 per cent. milk. The flies were used in experiments when 3-6 days old.

Insecticides.

The toxicants used were p,p'DDT, 1-methylnaphthalene, and pyrethrins. Solutions of the first two were prepared from the pure compounds, and of the last from a concentrate, viz., 25 per cent. w/w pyrethrins (as determined by the A.O.A.C. method) in Shell Risella oil 17. Solutions were made up in the refined petroleum oils, odourless distillate (O.D.), Shell Risella oil 17 (R17), or Liquid Paraffin B.P. At 20°C., the viscosities of the oils are, respectively, 2.5 cp. (approx.), 20 cp. (approx.), and much greater than 20 cp. O.D. is volatile at room temperatures, the other two oils are for practical purposes non-volatile. For a specification of O.D., see Hewlett (1947). The following are some of the characteristics of R17, the oil most used in the investigation: specific gravity (60°F.), 0.870; flash-point (closed), 310°F.; viscosity, Redwood I (70°F.), 125 sec.; initial boiling point, 290°C.

Toxicity tests.

In determining the toxicities of different liquids (which were coloured with Sudan IV where convenient), flies were treated topically on their mesonota. Volumes of 1 μ l. or more were administered with a micrometer syringe, and lower volumes with an improved form (see Hewlett, Belcher & Cordaroy, 1954) of the air-pulse micro-drop applicator described by Hewlett (1954). For dosage the flies were kept for a few minutes under carbon dioxide anaesthesia at 20°C. and 70 per cent. R.H. They were returned to 27°C. immediately afterwards to await a mortality count 24 hr. after dosage.

Confinement of flies for dosage by means of hanging drops.

Various devices bearing drops were hung in clean containers, cages, or chambers, into which flies were released. Exploratory experiments were carried out with single flies in small glass vessels, and with groups of flies in cages 19 in. high \times 18 in. \times 18 in. In these exploratory experiments the behaviour of flies was observed, including their reactions on touching drops; toxicities of doses collected were not determined.

In the main series of experiments, drop-bearing devices were hung in a chamber (well illuminated unless otherwise stated), 3 ft. high \times 3 ft. wide \times 2 ft. deep, as used by Parkin & Green (1945) for testing space sprays. The front of the chamber was of glass and the other internal surfaces were cream-painted; before an experiment the floor was covered with clean absorbent paper. A batch of about 100 or about 200 flies was introduced into the chamber, and left with access to the drops for 1 hr. The drop-bearing device was removed and the flies were left in the chamber for about $\frac{1}{2}$ -hr. longer. Tests showed that all flies that had received lethal doses were then knocked down (though the reverse was

not necessarily true); those knocked down were transferred to a muslin sleeve cage to await a mortality count 24 hr. after their release into the chamber. The remaining flies were counted and discarded.

One experiment was carried out in a larger well-illuminated chamber 12 ft. 5 in. long \times 8 ft. high \times 10 ft. Flies were released into the chamber, and given access to drop-bearing devices for 2 hr. The latter were then removed and the flies were left in the chamber with food to await a mortality count 24 hr. after their release.

Measurement of doses retained by flies.

The doses of liquid retained by flies after contact with hanging drops were estimated. In each experiment a solution containing 10 per cent. w/v pyrethrins was made by diluting the pyrethrin concentrate with one of the three oils mentioned above. A device bearing drops of the solution was hung in the smaller test chamber, into which flies were liberated. Most flies were knocked down 1-2 min. after touching a drop; as soon as a fly was knocked down it was captured and washed in 1 ml. of ethanol. The optical density of the yellow ethanol solution was estimated photo-electrically and the volume of solution retained by the fly was estimated through a calibration curve. This curve was constructed by determining the optical densities of solutions obtained by washing flies dosed with known volumes of the same pyrethrin solution, by means of the micro-drop applicator.

Results.

Toxicities of topically applied insecticide.

Flies were dosed topically with various volumes of 1 per cent. w/v DDT in R17 or 10 per cent. w/v 1-methylnaphthalene in R17. For the DDT solution the LV50 and LV90 were about 0.04 and 0.065 μ l. per fly, i.e., the LD50 and LD90 were about 0.4 and 0.65 μ g. of DDT per fly. This LD50 is near those obtained under comparable conditions by Busvine (1951) and Harrison (1954). For the 1-methylnaphthalene solution the LV50 and LV90 were about 0.03 and 0.08 μ l. per fly, i.e., the LD50 and LD90 were about 3 and 8 μ g. of 1-methylnaphthalene per fly.

The LV50 for R17 oil alone lay between 0.35 and 1.0 μ l. per fly, a more accurate determination being superfluous.

When the investigation was complete, a failure of the air-conditioning plant raised the breeding temperature of the flies. When normal breeding conditions were restored the flies were found to be highly resistant to 1-methylnaphthalene.

Suspension of drops.

A number of devices on which drops could be hung were tested, including pins, and small metal plates of various shapes, especially triangular. Flies appeared to collect large enough doses only from drops hanging on vertical or nearly vertical pins. Most flies attempting to alight on an oily surface seemed to be repelled, withdrawing abruptly and giving the impression of 'jumping back'.

In some of the exploratory experiments, pins were inserted into pieces of cork and drops of oil were deposited on the ends of the pins by spraying or dipping. The pieces of cork were hung in the small cages, each containing about 200 flies. The flies more frequently attempted to alight on the edge of a vertical lamina of cork than on its faces, confirming the observation of Pimentel, Schwaridt & Norton (1951) that flies settle more readily on narrow objects than on wide.

Flies appeared on the whole to collect larger doses from straight pins (fig. 1, a) than from curved or bent ones (fig. 1, b, c); probably the two latter gave a fly a greater chance of initial contact with the upper part of the pin, which was repellent because wet with oil, but from which the fly could not obtain a large dose.

These exploratory tests indicated that, for purposes of laboratory investigation, the most useful type of device on which to hang drops would be a rod bearing straight pins. Two series of rods bearing large numbers of pins were therefore made. Each rod (see fig. 2) consisted of an iron wire (3 mm. in diameter) covered with red polyvinyl chloride tubing. Headless, stainless steel entomological pins were set in the tubing in whorls of six each, each pin at an angle of about 20° to the axis of the rod, and adjacent whorls 5 mm. apart. Observation had



Fig. 1.—Different arrangements of pins tried in exploratory experiments with devices on which drops could be hung.

suggested that if the pins on the rods had been set appreciably more closely, many flies would each have removed more than one drop when attempting to alight on the rod. The rods of the first series were each furnished with 198 pins, 15 mm. long and 0.30 mm. in diameter, except for one rod, for which the pins were 20 mm. long and 0.45 mm. in diameter. The rods of the second series were each furnished with 696 pins, 15 mm. long and 0.25 mm. in diameter (as pins of this length and 0.30 mm. in diameter were no longer available).

In order to put drops on to the pins, a rod was dipped vertically into the liquid with the free ends of the pins downward, and pulled out fairly quickly. Each pin then retained a film of oil which soon afterwards ran down to form a drop. After being dipped, the rod was left for about 1 hr. before flies were given access to it, so that liquid had drained from the plastic tubing.

Volumes of liquid retained by flies.

Determinations by weighing showed that up to about 3 $\mu\text{l.}$ of any of the three oils used could be hung as a drop on the end of a pin 0.30 mm. in diameter held vertically. These determinations agreed with volumes calculated from the surface tensions of the oils. However, the volumes of liquid drops retained, after dipping, by pins set in the rods were found to be considerably less, being limited by the volume of the film of liquid adhering to the pin immediately after immersion. Rods bearing pins 0.30 mm. in diameter were dipped in solutions containing 10 per cent. pyrethrins, made by dilution with the different oils. For each solution, the volumes of 50 drops on pins randomly chosen were determined. The means (standard deviations) of the volumes were as follows: Liquid paraffin

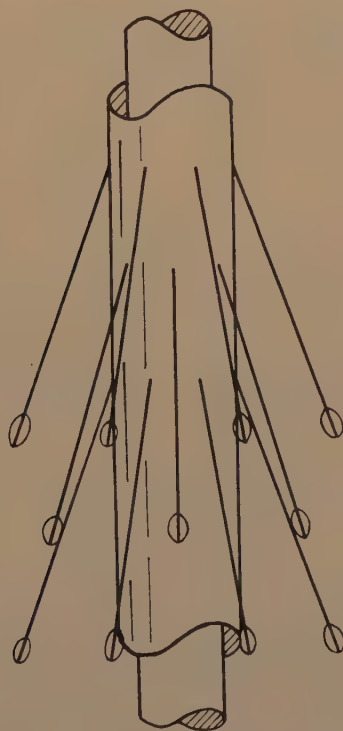


Fig. 2.—Schematic representation of a portion of a pin-bearing rod charged with insecticidal drops.

as diluent, 0.79 $\mu\text{l.}$ (0.28 $\mu\text{l.}$); R17, 0.62 $\mu\text{l.}$ (0.19 $\mu\text{l.}$); O.D., 0.74 $\mu\text{l.}$ (0.27 $\mu\text{l.}$). Similarly, on pins 0.45 mm. in diameter the mean volume (S.D.) for a solution of 10 per cent. pyrethrins in R17 retained was 1.47 $\mu\text{l.}$ (0.47 $\mu\text{l.}$).

In measuring doses retained by flies, a rod with 198 inserted pins, each 15 mm. long and 0.30 mm. in diameter, bearing drops of the pyrethrin solution under test, was hung in the small test chamber. Two hundred flies were released into the chamber, and the dose retained by each of the first 40 flies knocked down was determined. The results obtained when O.D. and R17 were the diluents for the pyrethrin concentrate are shown in fig. 3. The figure indicates the numbers

of flies retaining 0.0–0.1 $\mu\text{l.}$, 0.1–0.2 $\mu\text{l.}$ and so on. As might be expected, the volumes retained were very variable, but for each of these two oils the median volume retained was about 0.4 $\mu\text{l.}$ per fly. However, when liquid paraffin was the diluent for the pyrethrin concentrate the volumes retained by the flies were much smaller (median 0.1 $\mu\text{l.}$, approx., per fly). Reference to fig. 3 and the results of the toxicity tests (see above) show that a high proportion of flies could be expected to be killed by contact with drops of 1 per cent. DDT or 10 per cent. 1-methylnaphthalene in R17 on pins; 0.4 $\mu\text{l.}$ is 10 times the estimated LV50 for the former solution and 13 times that for the latter.

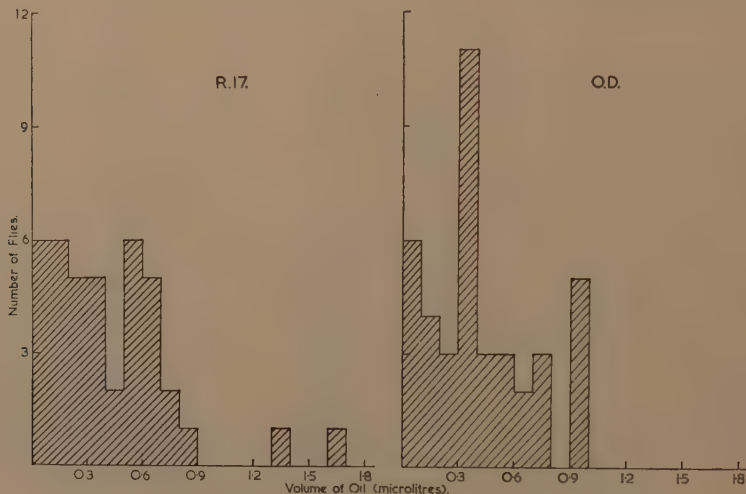


Fig. 3.—Frequency histograms showing the volumes of oil (Risella 17 or odourless distillate) containing pyrethrins retained by flies after being knocked down.

A rod bearing 198 pins 20 mm. long and 0.45 mm. in diameter was used next, and the volumes of pyrethrins in R17 retained by flies after contact with drops hung on the pins were determined as in the previous tests. The volumes retained by the flies were in fact much the same as those retained after contact with drops of the same solution on the smaller pins, 0.30 mm. in diameter.

Comparison of the doses of pyrethrins in R17 retained by the flies with the doses available to them on the pins of either size indicates that the flies lost a proportion of the doses that they originally took from the pins. Observation throughout the investigation showed that, after touching drops, flies shed some of their doses when alighting on the surfaces of the chamber, whichever insecticidal solution was used. In the measurement of volumes retained by flies, the object of using the pyrethrin solution was to achieve rapid knockdown, and so to minimise the quantities of oil lost and colour sorbed before capture, but, in fact, flight stimulation may have caused the flies to shed more of the R17 solution of pyrethrins than of the R17 solutions of the other insecticides used in the other experiments.

Liquid paraffin was evidently an unsuitable oil for insecticidal drops, in view of the small doses on the flies; O.D. was undesirably volatile; hence solutions of insecticides in R17 were used in all subsequent tests.

Over-all tests of effectiveness.

A straightforward test of over-all effectiveness can be quoted as an example. In the small chamber a batch of about 100 flies was given access for 1 hr. to a rod bearing 696 pins charged with 1 per cent. DDT in R17. In two replicate experiments the 24-hr. mortalities were 92 and 100 per cent.; the survivors were not knocked down. However, in similar experiments in which the flies had access to a rod with 198 pins charged with 2 per cent. w/v DDT in liquid paraffin, mortalities of 66 and 77 per cent., respectively, occurred, despite the small volumes presumably retained by the flies (see above).

In a larger-scale test 10 rods each with 696 pins were charged with 10 per cent. w/v 1-methylnaphthalene in R17, and hung from the ceiling of the large test chamber. The chamber was illuminated and its temperature maintained at $27 \pm 2^\circ\text{C}$.; the relative humidity was not controlled, but remained at about 45 per cent. A batch of 932 flies (3-6 days old) was released into the chamber. Two hours later, the rods were removed, but the flies were left. At 24 hr. after their introduction into the chamber, 930 (*i.e.*, 99.8%) of the flies were dead. Of 206 control flies kept within muslin cages in the chamber, only 1.4 per cent. were dead in 24 hr. About 30 ml. of insecticide solution was expended in this experiment, and less would have been if the solution draining from the rods after dipping had been collected.

Effects of light and temperature.

In the experiments described, the overwhelming majority of flies reaching rods hanging in the test chambers did so by flying. Hence any factor influencing flight activity could be expected to influence the number of flies collecting drops from the rods. To investigate the effect of illumination and temperature, batches of 100-200 flies were given access to rods bearing 696 pins charged with 10 per cent. 1-methylnaphthalene in the small test chamber. The chamber was kept well illuminated (general room illumination and a 100-W tungsten-filament lamp just outside the glass front) or in darkness; and at 20°C . or 27°C . The results are given in Table I.

TABLE I.

Effect of illumination and temperature on the percentage mortality* of flies with access to drops of 10 per cent. 1-methylnaphthalene.

	20°C .	27°C .
Illuminated	96.99	94.95
Not illuminated	15.29	26.35

* 2 replicates each of 100-200 flies.

As expected, the mortalities were much lower among the flies exposed in darkness than among those exposed in light; possibly a proportion of deaths among the former was attributable to flight during about 1 min. of low illumination necessary for their release into the chamber. However, under the same conditions of illumination the mortalities at 20°C . were about the same as at 27°C . At temperatures rather lower than 20°C ., hanging drops would doubtless be ineffective; Bucher, Cameron & Wilkes (1948) found house-flies at 10°C . to walk much more than fly.

Exhaustion of drops.

An experiment was carried out to estimate the number of flies that could be killed by drops from a rod before its insecticidal efficiency fell appreciably. A rod with 696 pins was charged with 10 per cent. 1-methylnaphthalene in R17 and hung in the small test chamber. Successive batches each of about 190 flies were given access to the rod by the normal procedure. The mortalities in the batches were respectively 98, 99, 97 and 82 per cent.; thus for the first 3 batches, in which 552 flies were killed, the insecticidal efficiency was high.

Persistence of insecticidal potency.

A number of rods, each with 696 pins, were charged with 10 per cent. w/v 1-methylnaphthalene in R17, and were stored at 27°C. and 65 per cent. R.H. After different periods of storage, rods were hung one at a time in the small test chamber, and a batch of 100 flies was confined with each rod by the usual procedure. The results, given in Table II, show that the drops on the rods remained highly toxic to flies for four weeks.

TABLE II.

Effect of storage on toxicity of drops of 10 per cent. 1-methylnaphthalene in R17.

Storage period (weeks)	Mortality per cent.	
	Treated	Control
1	85	1
2	88	0
3	93	0
4	92	2
6	26, 27	0

Discussion.

Both observation and the estimates of the volumes of oil retained by flies indicated that, under the conditions within the small test chamber, flies on alighting were liable to shed an appreciable proportion of the doses they had collected from hanging drops. However, a higher proportion might well be retained under conditions of practical control, owing to the greater space for flight. Within certain limits, the longer a fly flies after collecting a dose of oil from a hanging drop the further can the oil be expected to spread over its body surface, and hence the less is likely to be shed when the fly alights.

Although the laboratory experiments showed that hanging drops of insecticide can be highly lethal to flies, a considerable amount of development would be necessary before a method based on this principle could be used for practical fly control. Devices similar in effect to the pin-bearing rods that we used for investigational purposes, but such as could be manufactured commercially would have to be developed; however, there are many possibilities for doing this, and devices allowing automatic or semi-automatic regeneration of drops may be practicable. The efficiency and economics of drop-bearing devices would need to be compared with other methods such as adhesive and poison-bait fly-papers.

Hanging drops could of course be used in conjunction with other control measures such as treatment of walls with insecticide. The drops as a control measure appear to offer several advantages; a wide choice of contact insecticide, including a number of low mammalian toxicity which (unlike parathion for impregnating cords and bandages) could be handled by unskilled labour; economy of insecticide; and the feasibility of easy and frequent change of insecticide.

Summary.

Basic laboratory investigations have been carried out on a method for giving house-flies, *Musca domestica* L., relatively large doses of insecticide, with a view to possible applications in controlling, or preventing the appearance of, resistant strains of flies. The principle is that a relatively large drop of mineral oil will hang on the lower end of a thin vertical or near-vertical wire (*e.g.*, a drop of up to 3 μ l. on a wire 0.3 mm. in diameter), and a fleeting contact of a fly with the drop will generally transfer to the surface of the fly a substantial volume of oil. For investigational purposes pins were inserted obliquely into rods (*e.g.*, about 700 pins into a rod 60 cm. long), and drops of up to about 1 μ l. were formed on the ends of the pins by dipping the pin-bearing rods into solutions of insecticide in oil. In a typical experiment a rod with suspended drops was hung vertically from the ceiling of a chamber into which flies were released; flies then collected doses of insecticide when attempting to alight on the rod.

In order to select a suitable oil solvent, flies were given access to rods bearing drops of different oils containing pyrethrins, and the volumes of the oils on individual flies knocked down were estimated. It was concluded that Shell Risella oil 17 (R17) was a better oil for the purpose than Liquid Paraffin B.P.; odourless distillate (odourless kerosene) was too volatile.

High mortalities occurred in batches of flies with access to insecticidal drops under conditions in which the flies were flying actively; the expenditure of insecticide was low. As expected, low mortalities were obtained in batches kept in darkness, when flight activity was reduced. Probably many compounds not ordinarily employed as insecticides could be used as toxicants in hanging oil drops for killing flies. For example, drops of 10 per cent. w/v 1-methylnaphthalene in R17 produced high mortalities, and maintained high insecticidal potency for 4 weeks when stored at 27°C.

The results of the experiments were encouraging, though further development would be necessary before the method found practical application.

References.

- BUCHER, G. E., CAMERON, J. W. MACB. & WILKES, A. (1948). Studies on the housefly (*Musca domestica* L.). III. The effects of age, temperature, and light on the feeding of adults.—*Canad. J. Res. (D)* **26** pp. 57–61.
- BUSVINE, J. R. (1951). Mechanism of resistance to insecticides in houseflies.—*Nature, Lond.* **168** pp. 193–195.
- HARRISON, C. (1954). Genetical aspects of DDT-resistance in the housefly.—*1st int. Symp. Contr. Insect Vect. Dis., Rome 1954* pp. 235–252.
- HEWLETT, P. S. (1947). The toxicities of three petroleum oils to the grain weevils.—*Ann. appl. Biol.* **34** pp. 575–585.
- HEWLETT, P. S. (1954). A micro-drop applicator and its use for the treatment of certain small insects with liquid insecticide.—*Ann. appl. Biol.* **41** pp. 45–64.

- HEWLETT, P. S., BELCHER, C. & CORDAROY, M. A. (1954). Micro-drop applicator. —*Rep. Pest Infest. Res. Bd* 1953 p. 18.
- KEIDING, J. (1959). House-fly control and resistance to insecticides on Danish farms.—*Ann. appl. Biol.* **47** pp. 612–618.
- KILPATRICK, J. W. & SCHOOF, H. F. (1956). The use of insecticide treated cords for housefly control.—*Publ. Hlth Rep.* **71** pp. 144–150.
- PARKIN, E. A. & GREEN, A. A. (1945). The toxicity of DDT to the housefly, *Musca domestica*, L.—*Bull. ent. Res.* **36** pp. 149–162.
- PARKIN, E. A. & GREEN, A. A. (1957). Houseflies and blowflies. [In] The UFAW handbook on the care and management of laboratory animals, 2nd edn., pp. 847–858. London, Univ. Fed. Anim. Welfare.
- PIMENTEL, D., SCHWARDT, H. H. & NORTON, L. B. (1951). New methods of house fly control in dairy barns.—*Soap & sanit. Chem.* **27** pt. 1 pp. 102–103, 105, 112A, 112c, 141.
- WICHMAND, H. (1953). Control of multi-resistant houseflies.—*Nature, Lond.* **172** pp. 758–759.
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TRAPPING AS A MEANS OF STUDYING THE GAME TSETSE, *GLOSSINA PALLIDIPES* AUST.

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(PLATE XIV.)

	CONTENTS.	PAGE
Introduction	...	533
The country	...	534
The problems studied	...	535
Experimental studies		
Types of trap	...	536
Comparison with other methods	...	539
Biological studies		
Habitat	...	540
Activity	...	544
Host influence and swarming	...	545
The pattern of tsetse distribution in a squatters' settlement		
Catching-out effect	...	549
Penetration of fly into the settlement	...	551
Effect of land use	...	552
The effects of settlement	...	553
Experiences with other species	...	553
Discussion	...	554
Summary	...	555
References	...	556

Among the game tsetse, *Glossina pallidipes* Aust. is a species the population of which is particularly difficult to sample by the conventional means of fly-boys. In fact it can be so elusive to the human observer as to lead to the impression of its complete absence. There have been occasions in East Africa when the development of trypanosomiasis in cattle in supposedly tsetse-free areas has been the first intimation of the presence of *G. pallidipes*, and this has only been confirmed later by careful search with bait-oxen. The preference of this species for a number of hosts, such as dog, ox, porcupine and pig, rather than for man, was demonstrated by Vanderplank (1944). Chorley (1948) showed that even the scent of cattle dung and urine attracted this fly. Consequently it has been accepted that in searching for this species a bait-ox or a screen is necessary in order to overcome the insect's reluctance to show itself to man.

G. pallidipes has a very wide distribution throughout eastern Africa, extending from the north of Uganda down to Zululand; it can live up to an altitude of 600 ft.; and it utilises a variety of vegetation associations as its habitat. This species is of considerable economic importance, as a vector of trypanosomes pathogenic to cattle and also as the vector, together with

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G. morsitans Westw., of the East African form of sleeping sickness caused by *Trypanosoma rhodesiense*. It has received a great deal of study, but always the question of sampling has presented a difficulty.

33 101
An endemo-epidemic of Rhodesian sleeping sickness has been in existence since 1940 in an area of 400 sq. miles of forest and thicket country along the northern shores of Lake Victoria, extending from Jinja in Uganda to Port Victoria in Kenya. After the first fierce epidemic of 1940-44, with 3,186 cases, many of which were fatal, the disease had persisted as a dangerously fluctuating endemic varying from 20 to 120 cases per year. At the beginning of 1956, the writer, working with the East African Trypanosomiasis Research Organization, undertook epidemiological studies in this area. Apart from MacKichan's (1944) report on the first outbreak, there was little information available except for the records in the Uganda Medical Department's Annual Reports and files. It was not even known whether *G. pallidipes*, the vector in the initial outbreak, was the only species involved, since *G. palpalis* (R.-D.) and *G. brevipalpis* Newst. were widely present in the same area and apparently in contact with the affected population.

In West Africa, it had been shown that Morris's 'animal' trap (Morris & Morris, 1949) was more effective than boys in sampling the man-shy tsetse *G. longipalpis* Wied., which is similar to *G. pallidipes* in its habits and habitat, and trials by Glasgow (1958) in the Lambwe Valley in Kenya were showing that these traps caught the latter species readily. Consequently it was decided to see if traps could be used for obtaining entomological data in the *T. rhodesiense* investigation. In a study of this nature, moreover, the contact between man and tsetse is one of the most significant factors, and large numbers of observations are therefore required, from different areas and taken continuously over long periods, of a degree of standardisation which will make comparisons valid. For this purpose traps seemed eminently suitable, being easy and cheap to operate at a number of different places simultaneously and giving a standard measure of tsetse incidence in which variables due to the human observer were largely eliminated. The investigation lasted from March 1956 to December 1957, when it was prematurely terminated. Although such a short period is inadequate for this type of biological work, and there was not even time in East Africa for the full collation and analysis of results, yet a substantial amount of valuable data was obtained. The writer is indebted to the American Foundation for Tropical Medicine for the facilities afforded for the compilation of the data in the following paper.

The country.

The well watered, well forested country along the northern shores of Lake Victoria had been one of the most populous and productive areas of Uganda until 1901, when the first and most severe epidemic of sleeping sickness, caused by *T. gambiense*, struck it and within a few years wiped out two-thirds of the population. The catastrophe was checked, in 1908, by the complete evacuation of the population along the shores of Lake Victoria, since by then the vector was known to be *G. palpalis*, with a narrow littoral distribution. The evacuation was nominally of a 3-mile-wide strip along the lake shore, but because of the many indentations and creeks, particularly in Busoga District, the evacuated strip was often as much as 15 miles wide. This depopulated land rapidly filled with game and with *G. pallidipes*. Because of its natural attractions, however, it was gradually recolonised by settlers also, for the sake of the farming and fishing. This was the position, of contiguous communities of man and tsetse, which led to the fierce outbreak of *T. rhodesiense* in 1940. Again for lack of effective but less drastic control measures the population was

evacuated, this time from a zone, 5 to 20 miles wide by 50 miles long, stretching from just east of Jinja to Mjanji on the Kenya border.

When the present work was undertaken, the area held almost unbroken natural vegetation, the typical semi-deciduous rain-forest of the lake shore being more extensive on the western side and replaced eastwards by large tracts of drier *Combretum* savannah or deciduous thicket. The rain-forest was in various stages of regeneration, from 15 to 50 years in growth, and clothed mainly the ridges and slopes, the valleys holding open *Acacia* grassland, or papyrus swamps close to the lake. The contact between forest and grassland was rarely abrupt, there being more usually a transition zone in which tongues and clumps of dense thicket extended from the forest edge for distances of 20 to 100 yd. into the grassland. It was found that this ecotone (Pl. XIV, fig. 1) was the most favoured habitat of *G. pallidipes*.

G. pallidipes was the most abundant as well as the most widely distributed species of tsetse present, its greatest concentrations occurring in the broken-thicket ecotones just mentioned. It utilised extensive areas of thicket less readily as a habitat, did not appear to use high, closed-canopy forest at all and was completely absent from the populated and largely cultivated country outside the evacuated area even when this held apparently suitable vegetation. *G. palpalis* was much less abundant and was confined to the lake-shore forest and to the dense evergreen vegetation along inlets and a few wet depressions inland. It did not occur in papyrus swamps. *G. brevipalpis* was widespread but less abundant than the other two species and found only in or close to closed-canopy forest.

Game animals, rodents and small Carnivora were plentiful, since this was a sleeping-sickness area closed to human occupation, and the only hunting that went on was poaching. The following possible hosts for *G. pallidipes* were present:—elephant, *Loxodonta africana*; buffalo, *Syncerus caffer*; waterbuck, *Kobus defassa*; bushbuck, *Tragelaphus scriptus*; blue duiker, *Philantomba caerulea*; red duiker, *Cephalophus natalensis*; bush-pig, *Potamochoerus porcus*; hippopotamus, *Hippopotamus amphibius*. Crocodiles were not common in the lake, but *Varanus niloticus* was common along the shores, although elusive. There is no doubt that the comparative protection afforded these animals by the nominal exclusion of humans from the closed area since 1942–44 had caused a great increase in *G. pallidipes* during the past ten years or so.

At the time these studies were begun, human contacts with *G. pallidipes* which were responsible for maintaining the endemic of *T. rhodesiense* were being incurred in three ways: by the excursions into the closed forest of people living close to its borders, for gathering timber, firewood, fruits, etc., or to buy game-meat or fish, by hunters and fishermen forming temporary camps, and by a few illegal squatters' settlements well hidden within the forest. Of these three types of contact the settlements, since they were permanent and contained from 200 to 400 people each, were thought to be far the most dangerous from the point of view of sleeping sickness. Consequently one of the largest, at Busakira, 25 miles east of Jinja and just south of the village of Ikulwe, was chosen as the location for the main investigations.

The problems studied.

Examination of the data for human trypanosomiasis from 1940 onwards, and of the distribution of *Glossina*, made it clear that *G. pallidipes* was the main, very probably the only, vector, and therefore the species on which to concentrate. The descriptions of the trapping experiments, therefore, will always refer to this species, unless otherwise stated.

The ultimate aim of this research was to study the relation between the

tsetse and the inhabitants of a typical squatters' settlement, and the effect on the tsetse of a pilot scheme of controlled settlement, the South Busoga Resettlement Scheme, which was undertaken by the Uganda Administration, at the writer's suggestion, for reclaiming land from *G. pallidipes*. With these practical aims in view it was advisable to economise in time and effort by planning the research so as to combine, whenever possible, experiments on trapping methods with the collection of data relevant to the main objective. Therefore a series of studies was started, in March 1956, designed to cover the following groups of objectives:—

1. Experimental: experiments on the most suitable size, colour, position, etc., of traps; comparisons of traps with boys or other methods of capture.

2. Biological: observations on the tsetse's distribution, habitat, seasonal incidence, activity rhythm and movement.

3. Epidemiological: studies of the patterns of man/fly contact in the existing Busakira settlement and in the area of the new Resettlement Scheme.

A strict routine in trapping was established to ensure that data from different experiments should be comparable and that there should be no interruptions in its collection. A team of trained trap-boys lived in a semi-permanent camp within the fly-infested area close to the old and the new settlements, with sufficient personnel to ensure that sickness or accident would not interrupt continuous routine observation on all trap rounds. On the trap rounds, materials and tools for repairs were carried, and spare traps were available in the camp for replacements. In each round, trap sites were clearly marked by numbered pegs and remained constant throughout the experiment, the traps being circulated weekly on a rotation around two, three or four sites, to give site values free from individual trap bias. When comparisons were made between different types of traps, these were circulated over groups of sites with comparable site values. Except for certain experiments, which will be described below, traps were visited daily for five days a week, and when comparisons are drawn between different localities and times it is always on this basis. The writer spent much time in the area during the early experimental work; later, when the work had become a matter of routine observations, an average of two visits a month was made. A Resettlement Officer, Mr. J. Flemming of the Uganda Administration, lived permanently in Ikulwe and gave most valuable assistance and encouragement to the staff whenever this was needed.

Experimental studies.

Types of trap.

The first consideration was to see if any modifications in the standard pattern 'animal' trap would be advantageous in the work undertaken with *G. pallidipes* in Uganda. A series of eight sites was marked out in habitat of this fly, and different types of trap were circulated around these sites in two identical groups of four traps each, at least one standard trap being in each group. The following modifications were tested:—

Size of cage.—Shortening the catching cage, to 18 in. long instead of 24 in. (Pl. XIV, fig. 1), had several advantages, in economy of material and in ease of manipulation, especially in facilitating adjustment of the entrance slit to exactly the right width, a matter of the greatest importance to efficiency in catching. The short cage did not affect the trap's performance, as the following figures show, and therefore it was used in all subsequent traps.

Aggregate catches of *G. pallidipes* in eight trap-weeks.

2 traps with 18-in. cage	187 flies
2 traps with 24-in. cage	194 flies

Colour.—Trials over 14 months with traps covered with black hessian against the standard brown sacking gave the very interesting results shown in Table I.

The table shows the over-all superiority of black traps to brown, which was greatest during the rains but disappeared in the dry season. The explanation lies in the concept of this trap as representing a natural host of the tsetse, a concept which was responsible for the original design of the trap in the Gold Coast in 1940. As representing a host, the black trap attracts more flies through its being more conspicuous, a character which becomes more marked as the rains bring on the growth of grass and additional leaf cover. At this season the black traps were always more obvious to the human eye than the natural-coloured hessian ones in the actual trapping sites, although the area immediately around the trap was kept clear of grass and herbs. In the dry season, when the grass is flattened and eventually burned, light traps become as conspicuous as the black, and against a background of charred vegetation

TABLE I.

Total catches of *G. pallidipes* in brown and black traps during a 14 months' trial in South Busoga, Uganda.

Weeks	1956	Two brown traps		Two black traps		Black/ brown	
		Total	♀♀ (%)	Total	♀♀ (%)		
1-9	May-June	188	78	395	84.5	2.10	heavy rain
10-18	July-Aug.	148	84.5	231	80	1.56	moderate rain
19-27	Sept.-Oct.	113	81	155	79	1.37	light rain
28-35	Nov.-Dec.	211	87	118	86.3	0.56	dry
1957							
36-44	Jan.-Feb.	317	86.5	313	87.7	0.99	dry
45-53	Mar.-Apr.	369	89	677	85	1.84	early rain
54-61	May-June	252	81	423	75.5	1.68	heavy rain
Total 14 months		1598	84.7	2312	82.3	1.44	

after a grass fire they stand out much more clearly. Support for this feeding-response concept is given by the sex ratio of the catches, in which the female percentage increases for both colours of trap in the dry season, the time when the flies' frequency of feeding tends to be almost double that in the rains (Jackson, 1949), and the proportion of hungry flies in the population is consequently greater. As Morris & Morris (1949) pointed out, if this trap represents a natural host it attracts hungry and also non-feeding inquisitive males, but only hungry females. Thus when the proportion of hungry flies is greater, the ratio of females in the catch would be expected to rise, which, in fact, it does.

Smith & Rennison (1958) put forward a view that this trap has some of the attributes of the resting sites of *G. pallidipes*, but without any very clear arguments. Such a theory would not explain the dry-season feeding response (the increase in female percentage) shown in Table I, nor would it explain the supremacy of black traps in the rains, when the abundance of shade would reduce the high value of a dark colour in relation to its surroundings that is held in the dry season, without reducing its visibility as a target, or potential host. Good sites, it must be remembered, were in the open, not under shade.

Size.—It was soon apparent that *G. brevipalpis*, which was present in the experimental areas, was not coming readily to the standard-size traps. Hippopotamuses were known to be favoured hosts of this tsetse, which also attacks cattle more readily than man. Therefore two double-size traps, 4 ft. long by 2 ft. deep in the belly and standing with the shoulder 4 ft. from the ground, were made and tested. One was covered with normal brown hessian, the other with hessian painted dark grey, much the colour of a hippo. Although these traps were no more successful than the standard size in attracting *G. brevipalpis*, their catches of *G. pallidipes* were almost three times greater.

The uniform sex ratio in the different traps indicates that the superiority of the double or 'hippo-sized' traps must be absolute, a clear gain in catching power. This will, in part, be due to increased visibility, especially because of the added height, since the superiority became more pronounced with the growth of grass and leaf cover. The ratio of double- to standard-trap catches was 1:2.77 in May and June, with the grass level in general below 3 ft. high, and 1:3.08 in July and August with the grass level well above 4 ft. The figures as they stand

TABLE II.

Aggregate catches of *G. pallidipes* in 15 weeks' trial, May-Aug. 1956.

	Total flies	♀♀ (%)	Average per trap	Average light + dark
2 standard traps, brown ..	302	82	151	201
2 standard traps, black ..	503	82	252	
1 double trap, brown ..	704	80	704	585
1 double trap, dark grey ..	466	81	466	

give the impression that the colour preference found in standard traps was reversed in the case of the large traps, with the 4-ft. brown hessian trap catching 50 per cent. better than the 4-ft. dark grey one. Examination of the data in detail, however, showed that this superiority was greatest in the first six weeks, after which the catches of light and dark traps became almost equal, and after ten weeks the dark trap began catching better than the brown one, and this superiority was maintained from that point onwards. The conclusion is that the paint with which the dark grey trap was treated had a repellent effect on the tsetse which lasted for ten weeks or more, and that without this effect the darker trap was, in fact, the more attractive. The numbers of *G. pallidipes* caught during the first two months of the experiment was much greater than during the final six weeks, which would weight the data in favour of the unpainted light trap during the period that the repellent effect of the paint lasted. Without this early disadvantage in one of the double-sized traps it can be seen that their superiority over standard traps would be even greater than that shown in Table II.

The demonstration was conclusive and leaves no doubt that if large catches of *G. pallidipes* are required the larger trap is the more effective instrument. This model was not adopted in the South Busoga investigation, however, partly because the results appeared only after the main experiments were laid out with numbers of standard traps and it was not desirable suddenly to change the technique, also because the 4-ft. trap is more expensive to make, more difficult to standardise and much more difficult to carry about, particularly in

dense bush. When sampling can be done with small numbers of traps, however, these disadvantages would be outweighed by the better samples obtained.

Height.—Since the superiority of the double trap might be due in part to its being more easily seen in tall grass, a trial was made during a period with tall grass, above 3 ft. high, with traps of standard size built with long legs, to raise the shoulder of the trap 4 ft. from the ground. In 12 weeks' trial with one black and one brown hessian trap 4 ft. high against two black and two brown traps, standard size, *i.e.*, 2 ft. high, there was no difference in the performance of the traps at the two different heights:—

4 traps 2 ft. high caught	554 examples of <i>G. pallidipes</i> ,	trap average	113.5
2 " 4 " " " " " " " " " "	210 " " " " " " " " " "		105

Comparison with other methods.

Direct comparison of traps with fly-boys is difficult to make, since two boys, walking, cover a much bigger area than is tapped by two traps, whereas the traps work for 24 hours a day and seven days a week against the more limited time worked by fly-boys. A reasonable and practical comparison would be between a trap round which can be supervised by a single trap-boy every day with the catches made by a team of 2 fly-boys covering the same area. For several reasons fly-boys work best in pairs, so a pair will be taken as the unit for comparison.

In a heavily infested belt of *G. pallidipes*, in April and May 1956, a six weeks' comparison was made between eight traps, easily supervised by one boy clearing them five times a day, and a fly-boy team of two, making morning and afternoon rounds on six days a week. The traps caught 1,586 flies with 82 per cent. females, the boys caught 165 flies, with 13 per cent. females. This trap-round/fly-boy ratio of 9:1 was typical with fly at high densities. At low densities the ratio was less disproportionate, in the nature of 3:1, but numerically the traps continued to give much better samples, the fly-boys often failing to locate flies when they were coming to traps. Thus in a 5-week trial in September–October 1957, in very low density of *G. pallidipes* in Busakira Settlement, the following catches were made:—

Week	1	2	3	4	5	Total	♀ ♀ (%)
21 traps visited daily	3	2	6	6	13	30	73
2 boys, 2 rounds per day	2	1	3	1	2	9	30

The low proportion of female flies, 10–30 per cent., in catches by fly-boys is typical of the game-feeding tsetse, and this failure to catch female flies is one of the weaknesses of this method of sampling. The sexes are known to emerge from puparia in approximately equal proportions, but female flies have a considerably longer life than males, and a wild tsetse population can be reckoned to contain 70–80 per cent. females. Trap samples showed from 67 to 87 per cent. females, the most frequent range being between 75 and 82 per cent., figures approximating very closely to the estimated proportion in the wild communities. The numerical difference between fly-boy and trap catches was largely due to the greater number of female flies making up the latter. Thus it can be seen that not only do traps make larger catches of *G. pallidipes* than do boys under identical conditions, which *a priori* indicates a better sampling method, but that traps are, in fact, taking more truly representative samples of the tsetse communities present.

The only other sampling method with which direct comparison was made was Chorley's bicycle screen used by the Uganda Tsetse Control Department. Comparisons for five months in 1957 showed that in 20 traps, situated along

12 miles of road traversing a heavily infested belt of *G. pallidipes* and taking monthly totals of 1,556 to 2,736 flies, catches were 5 to 15 times greater than those made by a bicycle screen making one traverse and return five days a week. Trap catches, moreover, showed a much smoother curve, without the considerable irregularities, due to weather, etc., shown by the screen. This comparison showed that trapping can provide a far closer and more reliable index of the number of *G. pallidipes* present than can the bicycle screen. This number of traps can be supervised by one boy on a bicycle, so that this greatly superior sampling method was no more costly nor troublesome to operate.

Biological studies.

Habitat.

As soon as it was found that the traps provided a reliable means of sampling populations of *G. pallidipes*, an investigation was started into the distribution of this tsetse in a typical section of fly-belt one mile east of the Busakira Settlement and well within the closed sleeping-sickness area.

At the start of the investigation, in April 1956, the area was comparatively undisturbed, and game was in consequence plentiful, with periodic visits from small herds of elephant and buffalo. *G. pallidipes* was present in good numbers. Twelve trap sites were marked out, eight of them in what was already recognised as a favoured habitat, the zone of broken thicket between forest and grassland. Two were sited at 25 and 100 yards, respectively, within closed forest alongside an old track which was at the time used more by game than by man. Two were in open grassland, at 40 and 80 yards from the nearest forest edge, the second being at the foot of a tall, solitary tree. The lay-out of the experiment is shown in the map (fig. 1). The eight thicket sites were as nearly as possible equidistant, at 25- to 30-yd. intervals. Traps were circulated around the sites, to give site values rather than trap values, and were visited five times daily at 3-hourly intervals from 7 a.m. to 7 p.m., that is, sunrise to sunset. In May, some traps were needed urgently for another experiment and were taken from the grassland and forest sites, but the thicket sites were kept under observation for 20 months. A remarkable consistency in the relative values of these sites was observed, until a major disturbance occurred in October 1956 with the development of the Settlement Scheme which turned the old track into a much used road. The first five weeks of observation, with traps in all sites, can, therefore, be taken as representative. The results are given in Table III, which must be studied in conjunction with the map.

It is quite clear that the forest itself was inhospitable to *G. pallidipes*. Even with a path, frequented by hosts, leading past the two forest sites the numbers

TABLE III.

Catches of *G. pallidipes* in five weeks, April-May 1956, in habitat studies in South Busoga, Uganda.

Trap site	1	2	3	4	5	6	7	8	9	10	11	12
Males ..	23	25	14	32	8	4	23	19	22	18	8	3
Females	94	106	114	185	19	10	149	179	137	106	34	17
Total ..	117	131	128	217	27	14	172	198	159	124	42	20
♀♀ (%)	80	81	89	85	70	72	86	90	86	85	81	85

of tsetse caught there was only two-thirds of those caught in comparable sites in open grassland. Site 5, 30 yd. within the forest, caught 12.4 per cent. of the numbers present at the edge (site 4), and site 6 at 100 yd. caught only 6.5 per cent. It seems probable that these were all introduced flies, and that *G. pallidipes* was not living permanently even at such short distances inside the forest, an interesting finding in view of the fact that the most plentiful hosts here, bushbuck, duiker and bush-pig, spent most of the daylight hours, when the fly was active, within its shelter. Moreover this was high, closed-canopy forest, sufficiently open in the lowest storey to afford quite good visibility and room for flight above ground level.

The open grassland was being used at that time much more freely by flies than the forest, the sites at 40 and 80 yd. (11 & 12, fig. 1) showing 33 and 15 per cent., respectively, of catches at the nearest thicket edge (2, fig. 1). Again the suggestion is that the flies were moving out from what can be seen to be their true habitat in the narrow zone of broken thicket around the forest edge. The catches here were remarkably consistent, with sites 1-3 on the projecting tongue of forest, with fewer thicket clumps, showing a lower density of fly than appeared around the body of the forest where thickets were well represented. In this sector it is noticeable that traps in the more prominent positions, off promontories in the forest edge (sites 4 & 7) or in a small glade between clumps of thicket (site 8), made markedly higher catches than those

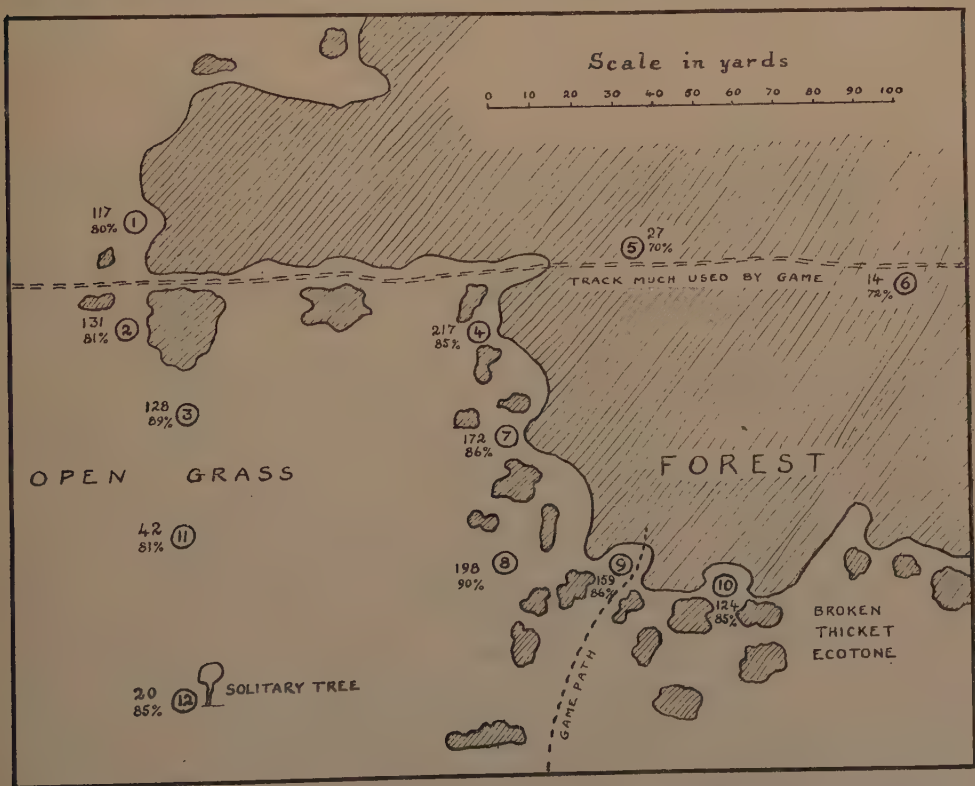


Fig. 1.—The habitat of *G. pallidipes* in the ecotone of broken thicket between rain-forest and grassland, close to Busakira, South Busoga, Uganda. Trap sites are shown by numbered circles, and total catches and percentages of female flies for a 5-week period, April–May 1956, are given.

TABLE IV.

The incidence of *G. pallidipes* in known habitat and in suspected habitat in adjacent secondary forest of about 15 years' regeneration in South Busoga, Uganda.

Period	1956			1957												52 weeks' aggregate Oct. 1956- Sept. 1957
	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
Rainfall (mm.)	145	48	66	29	45	138	336	221	118	113	55	45	56	71	97	
Total catch	479	578	275	262	368	395	362	146	120	116	111	154	125	105	150	3 66
Per trap-week	47.9	47.2	34.4	26.2	46	49.4	36.2	18.2	15	11.6	13.9	19.2	12.5	13.1	18.7	30.5
♀♀ (%)	74.8	77.8	78.5	77	79.5	78.7	73.3	74.8	72.6	74.2	79.2	79.3	76	73.2	76	76.6
Total catch	246	153	136	134	129	294	128	52	53	25	33	62	148	92	56	1445
Per trap-week	24.6	19.1	17	13.4	16.1	36.7	12.8	6.5	6.6	2.5	4.1	7.7	14.8	11.5	7	13.9
♀♀ (%)	76.6	68.5	56.6	69.3	66	73	64	57.8	50.8	80*	72*	78.8	70.8	65	80.3*	67.5
Forest as % of thick t	51	40.5	50	51	35	74.5	35.5	35.7	44	21.5	29.5	40	118	87.8	37.5	45.6

The total catches are made by a pair of traps in each vegetation type, and standardisation is to weekly catches per trap, with a total of 65 weeks' observation from October 1956 to December 1957.

(*) Percentages based on figures too small to be reliable.

placed in little bays in the bush, with restricted visibility although lying in typical habitat (sites 9 & 10). The propinquity of the game path undoubtedly raised the catch at site 9 in comparison with 10, and the same effect could account for the high value at site 4. Evidence of the effect of game in raising trap catches will be given in the section on 'host influence'.

The high forest around Busakira represented, as far as could be seen, the mature or climax vegetation of this part. There were in addition large tracts of younger secondary forest of about 15 years' regeneration, 30-50 ft. high, with frequent breaks in canopy, although the association itself extended unbroken over large areas except for occasional open, grass-covered valleys. In appearance this secondary forest was a vegetation-phase moister, denser and taller than the dry, deciduous-thicket habitat of *G. pallidipes* in eastern Busoga, intermediate between it and high forest. Parts of the area of the proposed settlement were covered by extensive stretches of this secondary forest, so it was necessary to examine its potentialities as a habitat of *G. pallidipes*. The area selected for this investigation was eight miles south of Busakira, on the road built for the settlement and new fishing port but in a section which was not developed, beyond road and bridge building, during the period of observation. Two traps were sited in the secondary forest, each in one of the small open spaces which occurred and which gave the trap a measure of visibility. These two sites were 400 yd. apart. Half a mile to the north, two trapping sites were chosen in true *pallidipes* habitat along the edges of a valley holding grass and thicket vegetation. The traps were rotated around these sites weekly, and observations were maintained, with five visits per week, for 15 months from October 1956 to December 1957. The results are shown in Table IV.

Unfortunately, farming from the new settlement encroached into the valley containing the habitat sites in October 1957, and this disturbance caused a pronounced fall in fly numbers here. The true value of this habitat, then, is based on the first 12 months' observations, October 1956-September 1957, and comparison between the two vegetation associations loses its validity after this period. The striking discrepancy in the figures in March 1957 for the secondary forest must also be explained here. It was due to the visit of a herd of elephants (see 'Swarming', below) which biased the trap average, sex ratio and comparison with thicket for the whole month, and increased by more than 10 per cent. the 12 months' average of flies per trap-week (f.t.w.).

Communities of *G. pallidipes* were evidently utilising this type of secondary forest as an all-the-year-round habitat, although at a density less than half of that measured in adjacent true habitat of broken thicket. (But for the visit of elephants in March 1957, which brought nearly 200 additional flies to the forest traps, the average per trap-week would have been just under 12 flies instead of 13.9.) The average density of 30 flies per trap-week measured in broken thicket was of the same order as that found in undisturbed habitat of this nature elsewhere (Table III), from which it would appear that secondary forest as a habitat is inferior to broken thicket, tolerated by this tsetse but not possessing all the advantages for a healthy fly community that the true habitat does. This view is supported by the greater irregularity in the monthly incidence in secondary forest, which falls to very low figures during 1957, and by the ratio of females to males being lower and less consistent than that seen in the true habitat. The significance of this low female percentage has not been interpreted, but it is taken as an unhealthy sign, as nowhere in well populated communities of *G. pallidipes* did such a low figure appear. On looking at the forest/thicket ratio (remembering the bias in March forest data) a tendency can be seen for the difference between thicket and forest population to become greater during the wet months, but this tendency is shown particularly in July and August which are, significantly, not the wettest months but those with the greatest leaf cover

in the forest. Since the two associations adjoin, this could be interpreted as a seasonal movement of fly out of a denser into a more open vegetation, a habit found in the Lambwe Valley by Johns (1958), although in this latter instance different plant associations were concerned.

The preference of *G. pallidipes* for the broken-thicket ecotone was confirmed at three other sites in the area of the new settlement, and these, together with the two experimental areas described above, were sampling a 12-mile transect through country infested with this tsetse. In all cases the fly densities in the broken thicket, as shown by traps, were of the same order, from 25 to 50 flies per trap-week, as long as the habitat remained undisturbed.

To summarise these findings, in this part of Uganda the true habitat of *G. pallidipes*, in which the communities reach their greatest numbers, is the narrow zone of broken thicket between the forest and the open grassland of the valleys, and young, regenerating forest with broken canopy forms a secondary and less favoured habitat, but high closed-canopy forest is not occupied.

Although this Uganda distribution conforms with Swynnerton's (1936) summary of his own and other people's experiences with *G. pallidipes*, it is at variance with the observations made by Moggridge (1950) on the Kenya coast. In this locality, very different both vegetationally and climatically from Uganda, *G. pallidipes* was evenly dispersed throughout all homogeneous vegetation communities, including regenerated forest and unbroken thicket, and showed no tendency to concentrate along the edges of thicket or forest. There was, however, a preference for the denser vegetation in the dry season, and a spread into lighter vegetation in the wet seasons.

Activity.

An enquiry into the activity rhythm of *G. pallidipes* was carried out concurrently with the initial study of its habitat by visiting the traps used in this experiment at 3-hourly intervals during the 12 hours of daylight, that is at 7, 10, 13, 16, and 19 hr. Considering only the eight sites in true habitat, the total catches during an 8-week period, April–May 1956, were distributed as follows:—

	♂♂	♀♀
7–10 hr.	15	22
10–13 hr.	73	868
13–16 hr.	234	603
16–19 hr.	111	139
19–07 hr.	7	3

This middle-day activity of *G. pallidipes* has been observed by Smith & Rennison (1958), with the peak in male activity occurring about two hours later than that of females, and Glasgow (1958), in the Lambwe Valley in Kenya, observed the female and male activity peaks at 14 and 16 hr., respectively, about two hours later than in Uganda. On the other hand, Moggridge (1949), working on the Kenya coast, found that, in savannah woodland, diurnal activity, which was generally similar in the wet and dry seasons, started on a large scale soon after light and increased to maximum proportions for an hour after daybreak. From that time, activity diminished until late afternoon, when it increased until sunset.

The important point about this activity cycle as demonstrated by traps is the extreme contrast between samples taken, even over 3-hr. periods, at different times of day. The above figures make it obvious that observations by means of fly-rounds or cycle screens, which last at most 3–4 hr., can give completely different pictures if made in the early morning, or at midday, or again in the

evening hours. Unless the time and duration of the activity peak is known, and the fly round is designed to tap this period, its results may give a very misleading picture of the numbers of fly present.

Host influence and swarming.

A general experience in trapping tsetse is that the rate of catching is greatly increased by the presence of the flies' natural hosts in close proximity to the traps (Morris & Morris, 1949; Buxton, 1955, pp. 509-511). Striking demonstrations of this phenomenon were obtained with *G. pallidipes* in South Busoga.

In the new settlement, one trap was sited in the cleared ground around an isolated house surrounded by *pallidipes* habitat, the site being 30 yd. from the house and the same distance from the edge of uncleared bush. For the first five months of 1957, catches averaged 20 flies per trap-week, the range being 11-22 f.t.w. In June, a number of goats was introduced by the settlers and kept tethered in their clearing, some being close to the trap. The trap average was more than doubled, rising to 45.5 flies per trap-week in that month. The owners were made to remove their goats, and the catch immediately fell to 21 f.t.w. during July. This is a case in which the added stimulus of scent or sight, or both, brought out of their habitat flies which must have been present but not attracted by trap or humans alone.

Of a different nature but equally effective is the siting of traps in places, such as salt licks or game trails, regularly frequented by the normal hosts of *G. pallidipes*. Two cases of the latter have already been given in the preceding section and in fig. 1, in which sites near game paths gave catches 25 per cent. greater than did sites some distance away but otherwise similarly orientated. A more striking instance was obtained when siting traps in undisturbed broken thicket habitat in the area of the new settlement. At the beginning of November 1957, a trap was placed in what was thought would be a good site, at the edge of clumps of thicket in a valley where buffalo had been grazing recently. During two weeks only five female flies were caught. It was then noticed that 50 yd. away there was a track to a water-hole in the bush, much used by the buffalo and other game. The trap was moved to a site right alongside this track just where it entered the bush, and during the next three weeks catches of 54, 44 and 44 flies per week were recorded.

One of the most remarkable results of the trapping experiments in relation to game is the demonstration they have given of the existence of what can best be described as the swarm phenomenon in *G. pallidipes*. The presence of game, either from direct observation or from fresh spoor, was always noted by trap-boys in their daily trap records. In the two areas of routine trapping, the Busakira experimental area and the new settlement, buffalo and elephant were occasionally but not regularly present, and their trails could not be missed. When buffalo came into a trap area catches invariably rose, but not to such an extent that it could not have been due to the effect described above, of the sight or smell of the animals near the traps bringing out from the immediate environment flies which were not attracted by the traps alone. When elephants visited the area, however, the rise in the trap catches was phenomenal, of a magnitude which could only be explained by the elephant herds being accompanied by a swarm of *G. pallidipes* of both sexes, many of which entered the traps while the elephants were around and after they had moved on. The concept of a swarm, moreover, is supported by the fact that the phenomenon was strictly local, it affected only those traps which were right on the elephants' route or near which they had fed, leaving other traps, perhaps only 30-60 yd. off, with their catches only slightly raised or unaffected. The phenomenon was noticed every time elephants passed through an area with traps. Five of the most typical and fully documented examples will be given.

In the Busakira fly-belt, a small herd of elephants was present in April and

May 1957 and passed through the experimental area shown in fig. 1 on three occasions. On 6th April they moved down to the edge of the forest from the north, crossed the tongue of forest to the track, fed along this to site 4, demolishing the trap in the process, and then moved off across the open grass. The cage fortunately survived with its catch, and the trap was immediately replaced. The catches at this site were:—

14 weeks, 1st Jan.–5th April, 446 flies, average 31.8 per trap-week, 83.2% ♀♀
1 week, 6th–12th April, 305 flies, total 305 per trap-week, 80% ♀♀

A week's catch is quoted, for ease of comparison, but the incident is even more striking when the single catch recovered from the broken trap is considered, 238 flies taken while the elephants were there. The catches at sites 7 and 8 rose to 40 flies each during that week, against previous weekly averages of 27 and 25.8, respectively. The catch at site 9 was unaffected. Sites 10, 11 and 12 were no longer in operation.

A week later, on 14th April, the herd was back in the same patch of forest, they fed along the southern edge to the corner by sites 9 and 8, and then entered the forest opposite site 8. Catches at site 9 were:—

15 weeks, 1st Jan.–12th April, 377 flies, average 25.1 per trap-week, 86.6% ♀♀
1 week, 13th–18th April, 130 flies, total 130 per trap-week, 82.4% ♀♀

In the case of site 8, the catches were:—

15 weeks, 1st Jan.–12th April, 387 flies, average 25.8 per trap-week, 86.2% ♀♀
1 week, 13th–18th April, 146 flies, total 146 per trap-week, 87% ♀♀

Again the majority of the flies in each trap were taken on 14th April, the day of the elephants' visit, but the week's catch affords comparison. After this visit a general increase in the average catches was noticeable in all the sites in this area, which may have been seasonal although the possibility cannot be ignored that more flies than were caught in the traps may have accompanied the elephant herd into this section. With 200 extra flies caught by a pair of traps in one day, an even greater number could have remained to augment the local fly population.

A month later, on 20th May, the herd was back again. They fed in the valley which is to the south of the map, moved up past site 8 and entered the forest between sites 7 and 9. Catches at site 8 were:—

4 weeks, 19th April–17th May, 170 flies, average 42.5 per trap-week, 86% ♀♀
1 week, 18th–23rd May, 307 flies, total 307 per trap-week, 84% ♀♀

Catches in the adjoining sites all rose sharply in the week of 18th May, but fell to their previous level in subsequent weeks. In sites 7 and 9, flanking the elephants' path but not on it, the previous 3 weeks' averages of 18 and 21 f.t.w., respectively, rose to catches of 53 and 60 f.t.w. after the elephants' visit.

Four miles south of Busakira, two traps were placed, in a valley flanking the new settlement and holding undisturbed *pallidipes* habitat, as controls against the traps within the settled area. The traps were sited here on 1st November 1956, and two weeks later, on 17th November, three bull elephants moved slowly down the valley past both trap sites. The catches (both traps) were:—

2 weeks, 1st–14th Nov., 78 flies, average 19.5 per trap-week, 72% ♀♀
1 week, 15th–21st Nov., 225 flies, total 112.5 per trap-week, 73.8% ♀♀

The last example comes from the two trap sites sampling the potential *pallidipes* habitat in secondary forest eight miles south of Busakira (see p. 543). On 18th March 1957, a herd of about 20 elephants spent some time in the area, coming through the bush from the valley to the north and emerging on the road which passed both sites, feeding in the forest close to each trap before they moved off down the road. Although these sites were 400 yd. apart they had been showing closely similar samples, both regarding their weekly trap averages of

13.4 and 14.2 f.t.w. and the sex ratio of their catches. On the day of the elephants' visit the traps took 78 and 99 flies, respectively. The two sites can therefore be considered together.

11 weeks, 1st Jan.-15th Mar., 307 flies, average 13.9 per trap-week, 67% ♀♀
1 week, 16th-22nd March, 229 flies, total 114.5 per trap-week, 76% ♀♀

After this the trap catches fell to their previous level. The effect of this visit is obvious in the monthly averages shown in Table IV, and has, in fact, raised the number of flies per trap-week from an average of 12 calculated for the 11 months excluding March, to 13.9 for the full 12 months, giving an unnaturally high value to this secondary habitat.

By tabulating the data from these five examples (Table V) the salient points in this swarming habit of *G. pallidipes* can be more easily appreciated.

TABLE V.

Trap catches of *G. pallidipes* in the presence of elephant herds compared with previous rates of catching. South Busoga, Uganda.

Case	Date	Place	Normal catch	Swarm catch	Swarm/normal
1.	6th April 1957	Near Busakira, site 4	31.8 (83.2)	305 (80)	9.6
2.	14th April 1957	Near Busakira, site 9	25.1 (86.6)	130 (82.4)	5.18
	14th April 1957	Near Busakira, site 8	25.8 (86.2)	146 (87)	5.66
3.	20th May 1957	Near Busakira, site 8	42.5 (86)	307 (84)	7.23
4.	17th Nov. 1956	Near new settlement	19.5 (72)	112.5 (73.8)	5.77
5.	18th Mar. 1957	Secondary forest	13.9 (67)	114.5 (76)	8.2

All figures are standardised to flies per trap-week with female percentage in brackets.

The compact nature of the swarms is well shown by these data from the Busakira fly-belt, which show the full effect of the elephants only in the traps situated right on their path, and the incident of the broken trap on 6th April provides a unique piece of evidence of the swarm being right among the herd. At the same time the eventual rise in catches in neighbouring traps, which usually occurred with a lag of a few days, shows that many flies are left behind and eventually spread through the adjacent habitat. Regarding the size of the catches, the only consistent relationship that appears is that the larger swarms, as shown by trap catches, have occurred in the places where the highest normal catches were recorded. Exactly how large the swarms were is impossible to estimate without further direct observation. Assuredly many more flies were present than is shown by trap figures, as can be told by the effect on sites neighbouring the one visited, and the continued large catches after the elephants had passed. Turning to the sex ratio, this gives more information. There is a remarkable similarity in the female percentages in normal and swarm catches. In other words the elephants are not attracting new elements of the local fly population untouched by traps (as in the case of traps *vs.* fly-boys); they bring an absolute increase in fly numbers with a composition closely similar to that already present in the area. The one exception is very significant. In example 5 the low female ratio of 67 per cent., characteristic for this type of secondary forest, rose on the elephants' visit to 76 per cent., which is the ratio prevalent in the true habitat

in the valley half a mile distant (Table IV), the locality from which the elephants had just come. If the swarm concept is correct, it is obvious that the swarm, once collected, will move along with the elephants, although the nature of the problem, the association of a man-shy species of *Glossina* with a host which is occasional and unpredictable in its appearances and immediately intolerant of disturbance, makes proof very difficult. Example 5, however, provides evidence which fits readily with only one explanation, that of a swarm of *G. pallidipes* following a herd of elephants even into a terrain to which they were not accustomed.

It is not difficult to visualise how a swarm of several hundreds of tsetse can be collected when it is remembered how big is the fly population as calculated by various observers. Glasgow (1958) gives a density of 250,000 males of *G. pallidipes* per sq. mile in the Ruma thicket of the Lambwe Valley. This would mean at least a million flies of the two sexes. The density in the South Busoga fly-belt is lower, and from comparable trapping data could conservatively be put at 200,000 flies per sq. mile. Suppose a moving herd of elephants is visible to the tsetse up to 22 yd. on each side of its path—not difficult in the country described and considering how much a herd will spread out. If the herd, with a 44-yd. visibility, took a straight course through a sq. mile of fly-belt it would be visible to one-fortieth of the tsetse population, that is 5,000 flies. If only one-tenth were attracted, this would give the elephants 500 flies per mile of traverse. Unless in flight, the elephants' path is never straight; in their meanderings they will tap much more than one-fortieth of the terrain they pass through. In a day's feeding a herd will travel many miles, and in the process flattens down the vegetation to such an extent as to form what amounts to chains of small clearings, admirable hunting and feeding grounds for the game tsetse. Moreover, the habitat of broken thicket favoured by *G. pallidipes* is also a zone of great attraction to elephants, with its abundance of creepers, fruits, etc., at heights within easy reach, so the herds, when feeding, will automatically spend much time in close contact with this fly. It can be seen that elephants moving in *pallidipes* fly-belt would have no difficulty in collecting thousands of these tsetse around them in the course of a day. It would almost certainly be what is called a rolling swarm, new flies being attracted all the time and others being left behind. That it will follow the herd into less suitable habitat is shown by example 5. It will certainly follow it across open grassland, as can be seen from example 3. What happens when a herd enters inhospitable high forest, or during the night, can only be learned from direct observation.

The liability of elephant and buffalo to be accompanied by swarms of the game tsetse, *G. morsitans* and *G. pallidipes*, and therefore to play an important rôle in their dispersal, has been known to practical workers on tsetse survey and control for a long time. It is mentioned in the first Annual Report for the Uganda Tsetse Control Department, that for 1947. In the north of the Gold Coast the writer found a close association between elephants and concentrations of *G. morsitans submorsitans* Newst., particularly towards the end of the rains when grass was high and the few places open enough to afford space for flight and a range of vision for the tsetse were the areas trampled flat by elephants in their feeding. These could be from a score of square yards to several acres in extent and were usually connected by elephant paths used by the fly also. In the flattened areas, tsetse were sometimes so numerous as to constitute swarms. Instances of swarms of *G. pallidipes* have been given to the writer (personal communications) by Messrs. J. P. Bernacca and T. W. Chorley, both with exceptional field experience of this species and of game in Uganda. Yet it seems to be a subject which has always evaded proof by the conventional methods such as fly-rounds. It is in the detection of this type of phenomenon that traps can be of considerable value, with their mechanical round-the-clock rate of

sampling and the ease with which a number can be kept in continuous operation with a minimum of disturbance to their surroundings. In trap samples the odd incident, the irregularity, may provide a key to an important biological event, provided it is not ground to obscurity in the deadly machines of the statisticians.

The pattern of tsetse distribution in a squatters' settlement.

The squatters' settlement at Busakira, containing 400 people, lay four miles south of the nearest village, Ikulwe, and a couple of miles within the closed sleeping-sickness zone of South Busoga. Thus it was set in forest which surrounded it on three sides, with a thicketed valley on the fourth. Although the settlement was compact it did not consist of a continuous area of open, farmed land; this occurred only in the centre. For the greater part it was made up of groups of huts, each in its patch of cleared and cultivated land surrounded by uncleared bush, thus leaving strips of standing forest or thicket between family holdings. Of the whole occupied area only about one-half was cleared. It appeared that there would be ample habitat for *G. pallidipes* right within the settlement: indeed this was the general opinion expressed to the writer at the beginning of this investigation, and it was held that only continuous cleared land, with no intervening strips or patches of bush, would make it safe from tsetse.

To investigate the incidence of *G. pallidipes* in Busakira, six houses were chosen in positions which represented varying distances from the true habitat of the fly at the edge of the settlement to deep within the settled area. At each house, three sites were pegged out, one in the open yard between huts (Pl. XIV, fig. 2), one in their banana plantation (Pl. XIV, fig. 3), and one in a field of low crops such as groundnuts, beans or cotton (Pl. XIV, fig. 4). In three of the houses the absence of low cultivation necessitated placing the third site in a cleared area at the edge of uncut forest. At each house, three traps of the standard pattern were placed and circulated round the sites on a 3-weekly rotation. Traps were visited daily between 4 and 5 p.m. For control observations, fly figures were taken from three traps selected at random from the group of eight being used for the biological studies in the comparatively undisturbed fly-belt a mile to the east (Pl. XIV, fig. 1). The observations were maintained continuously for 19 months, from the beginning of June 1956 to the end of 1957.

Catching-out effect.

The first, and quite unexpected, effect of trapping in Busakira settlement was a steep reduction in the numbers of flies caught during the first few weeks, the fall continuing at a diminished rate for two months, after which the rate of catching remained at the much reduced level, with comparatively minor fluctuations, for the next 12 months. This phenomenon is shown graphically in fig. 2, in which are plotted the weekly total catches from the 18 traps in the settlement for the first five months of the experiment, also the curve of these catches smoothed in 3's, and the smoothed curve for the aggregate from the three control traps.

Although the controls show a small decline in fly incidence during the first three weeks, this is temporary and is offset by complete recovery during July. In August, the incidence falls to about half the June-July figures, but shows a slow increase again from the end of September. The fall within the settlement on the other hand is precipitate, 85 per cent. during the steep decline of the first two months, and it persisted right through the July recovery of the population in the control. By the time this decline had levelled off in September, there had been a fall of 94 per cent., measuring the September-October average of 7 flies per week against the average of 117 flies per week for the first three

weeks of trapping. It is obvious that the flies in the settlement had suffered a catastrophe not affecting those of the control. It is necessary to consider whether this was due to trapping.

A catching-out effect was recorded by Morris & Morris (1949) in the north of the Gold Coast, where reductions in numbers, up to 75 per cent. in six weeks, took place when traps were newly placed in the feeding grounds of *G. palpalis* and *G. tachinoides* Westw. in localities where the main food of this tsetse was man. The same effect is being observed with *G. palpalis* in Liberia at the time of writing this paper. Even in the case of the game-loving *G. longipalpis*, the

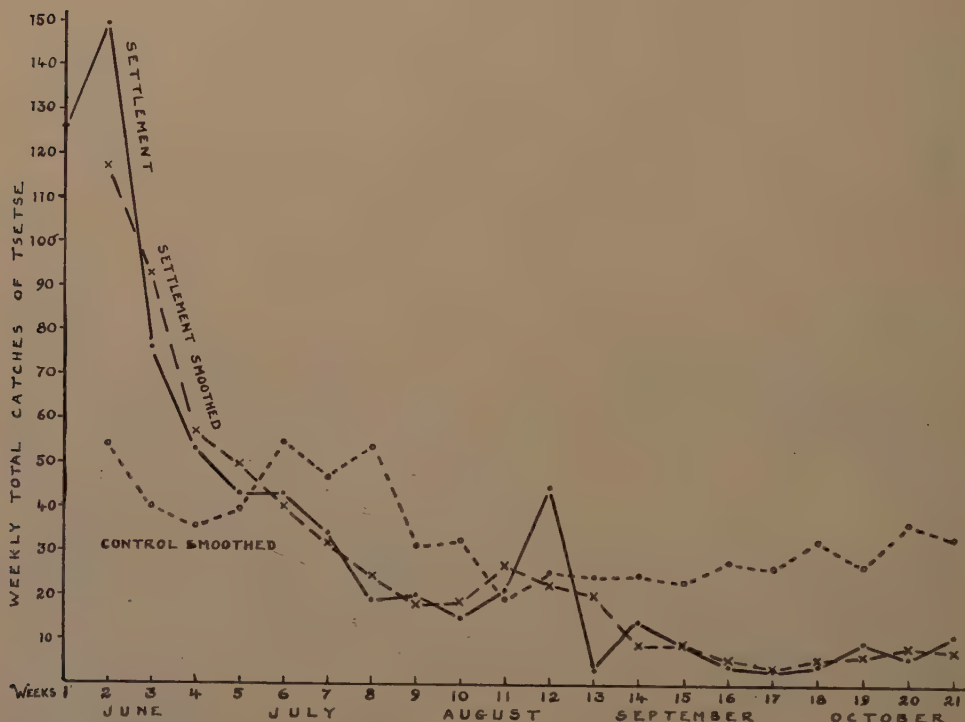


Fig. 2.—The reduction of *G. pallidipes* in a village, set in fly-belt, by means of trapping. The figures show weekly aggregate catches (both sexes) from 18 traps set within the settlement, plotted direct and smoothed in 3's, and catches from three traps in the control area a mile distant (smoothed in 3's).

author has observed a 50 per cent. fall in incidence in the first week of trapping in fly-belt of this species in the Gold Coast. In the present instance the striking reduction of *G. pallidipes* in Busakira can be explained as a catching-out effect if it is assumed that a proportion of the flies in communities of *G. pallidipes* are anthropophilous, a theory already suggested by the work of Glasgow and Johns (personal communications). The anthropophilous flies would tend to collect and stay near the constant sources of human food around the houses and farms. The limited numbers of these almost domestic flies would be as rapidly reduced by traps as in the case of the unquestionably anthropophilous *G. palpalis* and *G. tachinoides*. Subsequent catches could represent a steady but small intrusion of flies from the unselected and extensive population outside the settlement. There is in fact, a tendency for the settlement catches, once the

initial reduction has taken place, to follow the trends shown by the controls, with a lag of a few weeks, and this continued beyond the point shown in the graph. It will be shown, by further examination of the data, that this low level of catching represents the infiltration of *G. pallidipes* from the neighbouring fly-belt. Out of this continuous intrusion there could have arisen a specialised community of flies dependent almost entirely on man and resident around the village. It would be a limited and circumscribed community, vulnerable to reduction by trapping.

Penetration of fly into the settlement.

The data for the full 19 months is presented in Table VI, grouped into 3-monthly total catches except for the first month, June 1956. Because of the

TABLE VI.

The incidence of *G. pallidipes* in a settlement surrounded by fly-belt.

		Busakira houses (3 traps per house)							Control	
House number		1	2	3	4	5	6		Total (3 traps)	Average flies per trap-week
Approx. distance (yd.) within settlement		edge	100	200	400	800	1200	Total (six houses)		
Period	Weeks									
June 1956	4	221	52	25	13	9	54	374	5.2	262
July-Sept. 1956	12	160	58	15	8	22	7	270	1.25	800
Oct.-Dec. 1956	13	66	12	5	8	9	2	102	0.43	686
Jan.-Mar. 1957	13	87	17	15	8	4	10	141	0.6	1283
Apr.-June 1957	13	45	35	10	11	10	7	118	0.5	1646
July-Sept. 1957	13	20	18	9	7	3	6	63	0.27	390
Oct.-Dec. 1957	13	17	7	4	5	0	1	34	0.15	273
Total	81	616	199	83	60	57	87	1102		5340
Total (excl. June 1956)	77	395	147	58	47	48	33	728		5078
77-week average fly per trap-week		1.71	0.63	0.25	0.2	0.21	0.14	0.52		22

Catches of flies (both sexes) in groups of three traps at varying depths within the settlement and by three control traps in undisturbed habitat one mile distant.

bias in the first weeks of trapping, the June catches are discarded and the averages of flies per trap-week are calculated on the remaining 18 months' data, that is to say on samples in which the resident flies were not predominant.

House 1 is at the southern edge of the settlement where it is bounded by a valley with open grass and thickets, habitat for *G. pallidipes*. Houses 2 to 6 are at increasing distances from the fly-belt edge, with 6 at three-quarters of a mile within the settlement. The nice gradation shown, with the catches decreasing as the distance from known habitat increases, makes it clear that, once the semi-domestic anthropophilous tsetse were caught out, *G. pallidipes* was penetrating into the settlement from the fly-belt and was not living permanently in the strips and clumps of uncleared bush between the houses. It is evident, moreover, from comparison with the control catches made at a

distance of a mile, that a big reduction in the numbers of tsetse was being brought about by the presence and activities of a settlement of this nature despite its propinquity to permanent habitat of this fly.

Effect of land use.

Within a settlement such as Busakira there were four predominant types of land cover which might be used by *G. pallidipes* frequenting the settlement. They were:—the areas round the houses themselves, consisting of a level open yard with a group of thatched houses and granaries giving good shade; fields of low crops such as groundnuts, beans, cotton or sweet potatoes; the inevitable banana plantation, usually adjoining the compound and pleasantly shady, therefore for long suspect of holding fly; land cleared and not yet cultivated, always adjoining a strip of uncut forest and full of stumps, fallen trees and rank herbage. The first three types were well represented at houses 2, 3 and 6, and traps were maintained here for the whole period of 81 weeks, so their aggregate catches are strictly comparable. Cleared, uncultivated ground at the forest edge was represented at site 3 near house 1, close to the fly's habitat, and at sites 12 and 15, well within the settlement. Catches from these sites, which were associated with the three remaining houses not otherwise included in Table VII, are not, then, strictly comparable with the others, but they demonstrate the range of incidence of fly recorded in such places, and are therefore included.

TABLE VII.

The use made by *G. pallidipes* of different types of cultivation.

Period	Weeks	Between huts sites			Low crops sites			Bananas sites			Forest edge sites		
		4	7	16	5	8	17	6	9	18	3	12	15
June ..	4	10	5	11	23	0	39	19	8	4	78	4	2
July–Sept. 1956	12	19	3	1	29	5	5	10	0	1	77	18	4
Oct.–Dec. 1956	13	2	0	0	7	5	2	3	3	0	43	5	2
Jan.–Mar. 1957	13	0	2	0	12	4	8	5	2	2	60	2	4
April–June 1957	13	6	0	0	17	9	6	12	2	1	19	6	1
July–Sept. 1957	13	4	4	1	10	2	5	4	1	0	2	2	1
Oct.–Dec. 1957	13	0	0	0	6	5	1	1	0	0	0	3	0
Total	81	41	14	13	104	30	66	54	16	8	279	40	14
		68			200			78			333		

Total numbers of flies (both sexes) caught by traps in 81 weeks in the four types of land cover in Busakira settlement—the open yard between huts, fields of low crops, banana plantations, and cleared but uncultivated land at the forest edge.

The results of these observations are rather surprising, with open fields holding far more flies than do the shady and suspect banana groves, and these proving no more attractive than the open yard around the huts. When taken in relation to the findings in Table VI, however, this is understandable. After the first few weeks the flies caught are those penetrating into the settlement, not living within it, so are presumably hunting for food or mates. The range of visibility afforded by the open field evidently makes it more attractive to the wandering fly, the shade and humidity offered among the bananas being offset by the very restricted visibility. Again, the edge of strips of forest within the settlement, represented by sites 12 and 15, prove to be no more satisfactory for *G. pallidipes* than does an open field, a point of very great practical importance.

The effects of settlement.

The studies just described were designed to provide the knowledge required for planning a reclamation project, in which controlled settlement on the right pattern could be used to recover land occupied by game and *G. pallidipes* with a minimum of danger from Rhodesian sleeping sickness to the settlers. A full account of the South Busoga Resettlement Scheme will be the subject of a separate paper. A resumé appears in Morris (1958). It must suffice here to give only a summary of the rôle played by trapping in this undertaking.

In the first place the observations at Busakira gave a demonstration, invaluable in the early stages of getting the Scheme accepted, of the fact that a compact settlement in *pallidipes* fly-belt, even such a small one as of only 400 souls, automatically produced a zone of low incidence of fly in the area it occupied, most probably because of its disturbing effect on the game on which this fly was dependent for food. The new settlement was planned as a ribbon development, along 12 miles of road cutting through uninhabited bush, from the nearest Busoga town of Ikulwe to the abandoned fishing port of Kityerera on a gulf of Lake Victoria. It was held that opening up this port and encouraging every development possible, fishing, sand digging, timber extraction, coffee growing, etc., would result in so much disturbance of game that the effect on *G. pallidipes* would be sufficient to offset the additional lengths of exposed flanks in such a ribbon development. As soon as the road was pushed through to the lake shore, in October 1956, 16 traps were placed in the area, in pairs, each pair sampling a different type of terrain. Four pairs were sited in different parts of the new settlement, four were in adjacent unsettled fly-belt as controls. The traps were visited once a day on five days a week, and continuous observations were maintained for 15 months, from October 1956 to December 1957.

Altogether a series of observations of major practical value were obtained, in a scheme introducing settlement as a weapon against *G. pallidipes* in its rôle as vector of *T. rhodesiense*. Not only were the premises, based on the first experimental work in and around Busakira, fully justified, and a strip of good productive land recovered, but experience was obtained which could be of direct practical help in planning the control of this tsetse in other countries besides Uganda.

The full data will be presented in the paper describing the Scheme. It must suffice here to record that the traps gave conclusive evidence that where the settlement was compact it produced substantial reductions in the numbers of *G. pallidipes*, although these reductions were strictly local and did not extend beyond the areas occupied by the people's houses and their farms. Traps also showed the danger of an isolated position for a house, in the incident quoted in the section, "Host influence and swarming", above (p. 545), in which the introduction of goats brought in fly from surrounding undisturbed habitat and raised its incidence around that compound to the dangerously high level which was being recorded by control traps in undisturbed bush.

Experience with other species.

Traps had been used successfully by the author in studies of *G. nigrofusca* Newst. in West Africa, so it was hoped that they might be useful in sampling the related *G. brevipalpis* and *G. fuscipleuris* Aust. in Uganda. *G. brevipalpis* was quite common in the forest at the Busakira experimental area, and on dull days or in the evenings one or two specimens would nearly always be captured, following or entering a grey Land-Rover or, less readily, a light-grey Vauxhall car. In traps, however, the appearance of this species was sporadic and irregular; it certainly was not being attracted in proportion to the numbers present. Even the 'hippo sized' trap already described, 4 ft. high and 4 ft. long, did not prove

better than the standard pattern. When a fly-round with bait-oxen was introduced by the Tsetse Control Department this proved a far better sampling method for *G. brevipalpis* than did traps.

A three months' experiment in a valley infested with *G. fuscipleuris* in northern Ankole gave similar negative results. Four small traps and two large traps, each size in both black and brown hessian, were placed along the route of a fly-round using a bait-ox, maintained by the Tsetse Control Department, from October to December 1956. From a dozen to 30 examples of *G. fuscipleuris*, with sexes in approximately equal proportions, were taken on a traverse with the bait-ox, which covered about three times the area sampled by the traps. The six traps took only 2-3 flies per week. Fly-boys without any bait-animal, however, were no better in showing up the presence of this species than were traps.

During these experiments, and others specially set out close to E.A.T.R.O. headquarters in Tororo, traps were found to be effective in showing the presence of TABANIDAE. The following species were taken regularly: *Tabanus taeniola* P. de B., *T. par* Wlk., *T. gratus* Lw., *Ancala africana* (Gray), *Haematopota pallidipennis* Aust., and *Chrysops distinctipennis* Aust. Occasional captures of the following were made: *Tabanus xanthomelas* Aust., *T. brumpti* Surc., *T. ruwenzorii* Ric., *Haematopota coronata* Aust., *H. ugandae* Ric., *H. fusca* Aust., and *H. similis* Ric. These last four species of *Haematopota* were captured only in the large, 4-ft.-long traps; all the other TABANIDAE were attracted to both large and small traps equally well. In the case of the six species taken regularly, the seasonal fluctuations in their incidence were recorded in the E.A.T.R.O. cattle kraals and along a nearby river by means of a series of traps set out for this purpose.

Discussion.

The work on *G. pallidipes* in South Busoga has, admittedly, raised almost as many questions as it has solved. This is the nature of biological research, aggravated in the present instance by the curtailment of what had been planned as a long-term study. However, some further knowledge on the ecology of this elusive species of tsetse has been gained, and an advance has been made in the difficult problem of achieving its control. In the process, one important and fundamental principle in field research has been illustrated, the value of being able to obtain continuous records of the incidence of an insect in its natural environment with something approaching mechanical regularity and with a minimum of disturbance to that environment.

It is interesting to examine the reasons why traps appear to sample the populations of *G. pallidipes* better than do fly-boys. One of the most important factors working to the advantage of traps is their presence for 24 hours a day, for 365 days a year if required, in the locality being sampled, compared with the 3-4 hours' duration of a fly-round, which may sometimes operate only two or three times a month. Traps are in a far better position to detect the occasional, vagrant fly; in well-represented tsetse communities it is only necessary to examine the fly's daily activity rhythm to understand why the traps, always at hand to tap the full activity period whenever it should occur, take much truer samples of the numbers of tsetse present. An equal advantage lies in the fact that the samples are of a known degree of standardisation; they give a value (the flies per trap-week (f.t.w.)) has been used throughout the present work) which bears comparisons between localities and seasons. Irregularities at once show up, and are either due to a fault in the trap (which can easily be detected and which was eventually overcome by working the traps in pairs) or are an indication of a definite change in the environment. Added to these physical advantages of continuous and standardised mechanical sampling is the biological one which makes this form of trap so attractive to *G. pallidipes* and brings both sexes to it in such well-represented

numbers. The explanation of this attraction that conforms most fully with all the facts is that the traps represent a regular host of this tsetse whereas boys certainly do not. This weakness in fly-boy teams is got over by the use of a bait-animal. The physical disadvantage could only be overcome by organising repeated or lengthy fly-rounds during each day. The almost continuous presence of fly-boys with bait-oxen in the bush would defeat its own purpose, through the amount of disturbance caused to the fly's environment, in particular to its natural hosts, and the frequent introduction of artificial ones.

These are the intrinsic values of trapping, which make it particularly suitable for studying certain aspects in the ecology of tsetse which it has been found difficult to elucidate by other means. The swarming habit in *G. pallidipes*, and the utilisation by this species of different types of terrain, including a village and its cultivated land, are outstanding examples in the present research. To these advantages must be added the operative ones of staff and economy. One trap-boy with a bicycle can easily supervise 20-30 traps on daily visits, or twice that number on a 2-day rotation. The data from the latter would be slightly less accurate, owing to the escape of flies, which occurs more towards nightfall, but the great point is that, in trapping, the sampling still goes on, whatever the periodicity of the visits. The compensation for less frequent visits would be less disturbance to the habitat. According to the pattern of trapping chosen, the one boy could be responsible for anything from a close grid over a few acres to an extended transect of 10-12 miles. Above all, his results will be more reliable and more accurate than those produced by the much larger teams of fly-boys plus bait-oxen required to cover the same areas.

The admitted deficiencies in trapping as a sampling method provide a stimulus for further thought and research. The narrowness of the zone sampled by each trap is apparent from the incidents with elephants. Yet, in an extensive habitat, no local catching-out effect was shown, the numbers caught being maintained with great consistency over long periods; this shows that supplies of tsetse were being continually drawn to the traps. The greater catching power of the large, 4-ft. traps was possibly due to their sampling a wider zone than the small ones, a question being studied at the moment. Technical improvements to the traps, especially on the lines of further mechanisation and automatic recording, would unquestionably be of advantage. The outstanding ecological studies made by C. G. Johnson at Rothamsted, with his suction trap, demonstrate the value of an entirely mechanical sampling method. There can be dangers in mechanisation, however, if it is taken too far. The trap-boy's daily visits keep touch with the biological quantities in the environment; there is no excuse for translating results entirely in terms of the more easily measured physical constants, of temperatures and humidities, and thus reducing the tsetse fly to a mere bunch of tropisms. The Busoga experiences demonstrate that there is as much to be learned from a realistic interpretation of the modulations and breaks in an observed rhythm as there is from the steadily continuing rhythm itself.

Summary.

In an area of sleeping sickness due to *Trypanosoma rhodesiense* in Uganda, Morris's 'animal' traps were used to study the activity and the relations with habitat and hosts of the vector, *Glossina pallidipes* Aust., a tsetse difficult to sample by conventional fly-round methods.

This type of trap was found to give samples both numerically greater and more truly representative of the tsetse population present than did either fly-boys or Chorley's bicycle screen.

Black traps showed an over-all superiority to brown traps, greatest during the rains and disappearing in the dry season, and this was related to the tsetse being attracted by the trap as representing a natural host.

A trap of double linear dimensions made catches three times greater than those in standard traps.

Since trapping provided a standard measure of fly incidence, bearing comparison between different times and places of catching, it was used for determining the habitat preferences of *G. pallidipes*, its activity periods throughout 24 hours, and the influence of the presence of its hosts.

Evidence was obtained indicating that swarms of this tsetse, of magnitudes of at least two or three hundred flies, collect around and follow herds of elephants passing through fly-infested country.

In a squatters' settlement set in a belt of *G. pallidipes* in the closed sleeping-sickness area in South Busoga, a striking reduction in the numbers of tsetse took place during the first eight weeks of trapping, explained by there being resident anthropophilous flies within and around the settlement, which were rapidly caught out by the 18 traps in operation.

After the initial reduction, flies continued to intrude in very small numbers into the settlement from surrounding fly-belt. Surprisingly, these flies were caught more plentifully in open fields of low crops and in the open compounds of the houses than in the apparently more attractive cover of shady banana plantations.

The fact that such a settlement automatically lowered the numbers of tsetse in its immediate area in comparison with undisturbed fly-belt, gave support for a project for reclaiming a strip of country from *G. pallidipes* by means of settlement alone. The use of traps demonstrated that marked local reductions of fly incidence took place when the South Busoga Resettlement Scheme was put into operation, and provided information of value for wider developments on similar lines.

References.

- BUXTON, P. A. (1955). The natural history of tsetse flies.—*Mém. Lond. Sch. Hyg. trop. Med.* no. 10, 816 pp. London, Lewis.
- CHORLEY, T. W. (1948) *Glossina pallidipes* Austen attracted by the scent of cattle-dung and urine (Diptera).—*Proc. R. ent. Soc. Lond.* (A) **23** pp. 9-11.
- GLASGOW, J. P. (1958) Les pièges dans l'étude de *G. pallidipes*.—*6th Mtg int. sci. Comm. Tryp. Res., Salisbury 1956* pp. 31-33.
- JACKSON, C. H. N. (1949). The biology of tsetse flies.—*Biol. Rev.* **24** pp. 174-199.
- JOHNS, D. L. (1958). Some ecological factors affecting *G. pallidipes*.—*Rep. E. Afr. Tryp. Res. Org. 1956-57* p. 59.
- MACKICHAN, I. W. (1944). Rhodesian sleeping sickness in Eastern Uganda.—*Trans. R. Soc. trop. Med. Hyg.* **38** pp. 49-60.
- MOGGRIDGE, J. Y. (1949). Climate and the activity of the Kenya coastal *Glossina*.—*Bull. ent. Res.* **40** pp. 307-321.
- MOGGRIDGE, J. Y. (1950). The relations of the coastal tsetse of Kenya to the plant communities.—*Bull. ent. Res.* **41** pp. 301-315.
- MORRIS, K. R. S. (1958) Studies of *G. pallidipes* in Busoga, Uganda.—*Rep. E. Afr. Tryp. Res. Org. 1956-57* pp. 63-68.

- 37 110 MORRIS, K. R. S. & MORRIS, M. G. (1949). The use of traps against tsetse in West Africa.—*Bull. ent. Res.* **39** pp. 491–528.
- SMITH, I. M. & RENNISON, B. D. (1958). Studies on sampling methods for *Glossina* populations.—*Rep. E. Afr. Tryp. Res. Org.* 1956–57 p. 43.
- SWYNNERTON, C. F. M. (1936). The tsetse flies of East Africa.—*Trans. R. ent. Soc. Lond.* **84** pp. 1–579.
- VANDERPLANK, F. L. (1944). Studies of the behaviour of the tsetse-fly (*Glossina pallidipes*) in the field: the attractiveness of various baits.—*J. Anim. Ecol.* **13** pp. 39–48



FIG. 1. Trap, with shortened, 18-in., catching cage, in a good catching site in the broken-thicket habitat of *Glossina pallidipes*, 1 mile east of Busakira village, Uganda.



FIG. 2. Trapping site in the open ground between huts in squatters' settlement, Busakira.



FIG. 3. Trapping site in the banana plantation adjoining a group of huts in squatters' settlement, Busakira.



FIG. 4. Trapping site in a field of low crops (beans) close to a group of huts in squatters' settlement, Busakira.

A BIOLOGICAL AND ECOLOGICAL STUDY OF THE RICE
PENTATOMID BUG, *SCOTINOPHARA LURIDA* (BURM.)
IN CEYLON.

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(PLATES XV & XVI.)

Until the year 1940, the black rice bug or rice Pentatomid bug, *Scotinophara lurida* (Burm.), was recorded as being an occasional insect found on the rice crop in a number of parts of Ceylon. In that year, however, this insect appeared in very large numbers in rice tracts extending over an area of about 10,000 acres of the Left and Right Bank Colonization Schemes of the Walawe River in the Southern Province. It has also been recorded in large numbers at Okkampitiya, in the Uva Province, and Polonnaruwa and Minneriya in the North Central Province. In all these areas rice is grown entirely under irrigation and not under rain-fed conditions. Since 1940, the insect has periodically assumed epidemic proportions in the Walawe Schemes and has also appeared in increasing numbers in the other areas mentioned.

About 12,000 acres of rice are cultivated under the Walawe Right and Left Bank Colonization Schemes. Two crops are grown a year of, chiefly, locally selected pure-line varieties of rice requiring $3\frac{1}{2}$ to 4 months to mature. A seedling crop is in the field during the months of April–May and November–December and harvesting occurs in August–September and February–March. Fields in these areas lie fallow during the months of August–September and part of October and in February, March and April. Water is permitted by irrigation into the tracts during the months of April and October for preparatory tillage and sowing.

S. lurida is a major pest of rice in China and in Japan. The results of extensive studies on the biology and control of this pest in Japan have been reported by Katsumata (1929), Kawasi (1955) and Kawada & others (1954). De Alwis (1941) has provided an account of this insect in Ceylon. The increasing importance of the pest to rice cultivation in this country has necessitated more intensive studies on its biology, ecology and control. This paper presents the results of biological and ecological studies conducted during the past four years. The parallel studies conducted on the susceptibility of *S. lurida* to insecticides and its insecticidal control are published in a separate paper (Fernando, 1960).

***S. lurida* on seedling rice.**

Invasion of seedling rice tracts.

Adults of *S. lurida* (Pl. XV, fig. 1) leave their aestivation sites to invade the earliest sown rice in nurseries or broadcast tracts when the crop is about two to three weeks old. This happens during the months of April and May for the first crop and the months of November and December for the second crop. At dusk and at night the bugs are very active and are found in flight in large numbers, and they are much attracted to lights. This migratory activity continues until the crop is 1 to 2 months old, when copulation and oviposition are completed.

Bugs congregate on the stems and leaves of rice seedlings and, during very heavy infestations, as many as five to eight have been found on a single 3- to 4-week-old seedling plant. Such infestations were, however, never uniformly

distributed; they were heavier where the plants were closely packed and in those areas where the plants were greener and healthier. Even in infestations of low population densities the distribution of bugs followed the same pattern on the seedling rice. Another noticeable feature of the distribution of *S. lurida* on seedling rice is that plants on tracts having a few inches of water are preferred to those where no water is present at the base of the plants.

Diurnal activity.

During the early hours of the day, bugs are found feeding upon the upper parts of the rice seedlings and even upon the upper surface of the leaves. As the day advances and the intensity of the sunlight increases they migrate to the underside of the leaves and on to the stems. The bugs continue to feed during the day on parts of the plants shaded from direct sunlight and they have very rarely been observed to take wing during hours of daylight. During field evaluation of insecticides for the control of this pest it was found that all the bugs caged in field cages were not accounted for by those present upon the leaves and the stems of the rice seedlings or floating dead upon the surface of the water. Careful examination of the basal parts of the rice seedling stems below water-level showed that several bugs were adhering to those parts of the rice seedling which were under water. This observation was checked more carefully under natural field conditions. Bugs usually take cover rapidly or even drop into the water when disturbed. However, the possibility of disturbance being responsible for the bugs being found below water-level was eliminated by approaching observation points in the field with the greatest caution. The further possibility that bugs were found below water-level owing to sudden fluctuations in the water-level of race tracts could be eliminated because tracts where the water-level was stable for the previous 24 hours were selected for the observations. Data were taken of the number of bugs upon the leaves, on the stems near water-level and below it. In 20 separate counts at 8 a.m., the distribution on leaves and on the stems above water-level and below it was 52.22, 39.44 and 8.33 per cent., respectively. The corresponding figures for counts taken at 11 a.m. were, 48.2, 42.1 and 9.7, respectively. These data, it will be seen, indicate no relationship between the time of day or intensity of sunlight and migration of bugs below water-level on rice seedlings.

Experiments were conducted in the laboratory to assess the survival of *S. lurida* under water. The basal 4 inches of 6-week-old rice seedlings were planted in one inch of rice-field soil, in glass dishes 6 inches deep. Adult bugs were then placed on these planted rice stems and allowed to feed for about two hours. Water collected from a rice-field was then introduced into the glass dishes gradually until the stems of the rice seedlings were completely submerged. Bugs were removed from the water at hourly intervals and maintained on rice seedlings for observation of survival. The results in Table I show that some adults of *S. lurida* could survive up to 7 hours continuous immersion in rice-field water without showing any noticeable ill effects up to 24 hours later. The experimental conditions, however, were not an exact duplication of field conditions as the bugs were forced under water and their first response to the immersion was secretion from the stink glands.

Nocturnal migrations.

Whereas during hours of daylight *S. lurida* is very sluggish and rarely ever takes wing, at dusk, bugs on the seedling crop become very active. This marked difference between the diurnal and nocturnal activity of *S. lurida* is only apparent in the generation of bugs migrating from aestivation sites on to the seedling rice and lasts until oviposition. Feeding continues during the night.

***S. lurida* on maturing rice.**

As the crop grows older, the bugs restrict their movements and feeding to the basal stem region of the plant. If no water is present on the rice tracts they will be found on the soil among the short weeds, grasses or debris surrounding the base of the rice plants or along the basal 3-4 inches of their stems. Bugs are rarely found feeding on the upper portions of the stems of maturing rice plants or on the leaves of such plants. During heavy rains, however, when the plants are wet and very moist conditions prevail, adults can be found in small numbers feeding upon the leaves of maturing and mature rice plants. When the ear-heads are freshly formed the bugs can be seen feeding upon the grains, but they are not particularly attracted to the young ear-heads as the bulk of the existing bug population can be found at the base of the plants. Nocturnal flight activity is negligible at this stage of the crop, when compared to that of bugs on the seedling crop.

TABLE I.

Survival of adults of *S. lurida* after submergence in rice-field water for varying periods of time.

Duration of submergence (hr.)	Number of bugs used in test	Survival of bugs 24 hr. after removal from water (%)
1	40	97.5
2	60	78.3
3	30	70.0
4	30	63.3
5	20	60
7	20	35

Distribution of adults of *S. lurida* when crop is in the field.

The distribution of adults of *S. lurida* in the field depends to some extent upon the size of the population present at the time. Details of the distribution of the bugs at various seasons of the year and periods of different population densities of the pest are given in Table II. During preparatory tillage, when irrigation water has been introduced into the tracts, the bugs are found mainly on the bunds within rice tracts, patches of higher ground within and near rice tracts and on the edges of channels and other waterways near rice tracts during seasons of both high and low population densities of the insect. When the crop is on the field, however, the bugs concentrate within the rice tracts. The distribution of bugs outside the rice tracts depends to a large extent upon the size of the bug population existing at the time. During an epidemic of *S. lurida*, a relatively large number are to be found outside the rice tracts in locations such as on rice-field bunds, along irrigation channels, etc. During seasons of low population density, however, bugs are found almost entirely within the rice tracts when a crop is in the field.

Development of *S. lurida*.**Copulation.**

After feeding for about one week upon the rice seedling crop, bugs are observed in copulation in the field. With the next generation copulation is observed about

TABLE II.
Distribution of populations of *S. lurida* in and around rice tracts in relation to time of year.

Site	Bug population per sq. yd.					
	During epidemic of pest			During low population density of pest		
	When fields are fallow	During preparatory tillage	When crop in seedling stage	When crop ready for harvest	When fields are fallow	During preparatory tillage
On rice tracts	14A*-25N**	2A-—	125A-12N	40A-27N	3A-17N	9A-—
	13A-31N	6A-—	63A-60N	26A-14N	1.5A-2N	4A-—
	25A-17N	1A-—	57A-32N	13A-11N	0.25A-3N	2A-—
	11A-12N	2A-—	67A-52N	51A-18N	0.5A-12N	11A-—
On bunds	75A-12N	53A-—	3A-6N	12A-3N	7A-2N	10A-—
	37A-—	18A-1N	2A-3N	4A-5N	6A-1N	14A-—
	60A-—	12A-—	8A-14N	11A-—	18A-—	5A-—
	18A-—	21A-—	—-2N	23A-4N	12A-—	12A-—
Up to 8 ft. of edge of higher ground surrounded by tracts	32A-6N	17A-—	1A-3N	3A-2N	3A-—	10A-—
	17A-—	35A-3N	4A-7N	4A-1N	7A-—	1A-1N
	27A-12N	37A-—	2A-2N	—-2N	3A-—	5A-—
	11A-—	27A-—	4A-4N	11A-—	2A-—	17A-—
At centre of patches of higher ground surrounded by tracts	14A-—	11A-—	2A-1N	2A-1N	1A-—	5A-—
	3A-1N	3A-1N	—-—	1A-—	—-—	19A-1N
	2A-—	7A-—	1A-1N	—-—	—-—	17A-—
	2A-—	11A-—	2A-—	—-—	—-—	7A-—
On other higher ground	1A-—	2A-—	—-—	2A-—	1A-—	2A-—
	—-—	3A-—	—-—	3A-—	—-—	11A-—
	7A-—	1A-—	2A-1N	—-—	1A-—	—-—
	3A-—	1A-—	2A-—	1A-—	—-—	4A-—
On edges of channels and other waterways	2A-3N	7A-—	7A-2N	2A-1N	—-—	27A-—
	4A-2N	17A-—	4A-3N	3A-1N	—-—	9A-—
	13A-—	12A-—	6A-—	—-—	—-—	14A-—
	1A-—	9A-—	11A-—	7A-—	—-—	4A-—

* A = Adult.

** N = Nymph.

- = No insect.

the time the rice is entering the shooting stage. Copulation was observed at all hours of the day. Egg-laying commenced about 10 days after copulation was first seen.

Oviposition.

When the rice crop is in the seedling stage, oviposition is chiefly on the rice plants where the eggs are deposited upon the leaves or less frequently upon the stem. On the leaves of rice seedlings, oviposition is predominantly on the underside of the apical three inches of the leaves. Oviposition also occurs upon weeds, especially those within, and, to a lesser extent, those bordering rice tracts. Among the weeds, those belonging to the family Graminaceae, such as *Isachne globosa* and *Echinochloa crus-galli*, are preferred by *S. lurida* for oviposition. Other alternate oviposition sites are the leaves and stems of weeds belonging to the family Cyperaceae such as *Cyperus difformis*, *Cyperus flavidus*, *Cyperus iria*, *Cyperus rotundus*, *Fimbristylis miliacea* and *Fimbristylis dichotoma*, and also to the family Marsileaceae, such as *Marsilea quadrifolia*, and the family Pontederiaceae of which *Monochoria vaginalis* is frequently a host for oviposition. Under very windy conditions when the crop is in the seedling stage, egg-laying is mainly on the shorter, better protected grasses growing around rice seedlings, rather than on the rice seedlings themselves.

During the maturing of the rice crop, oviposition is mainly on leaf sheaths at the basal parts of the rice stems and to a lesser extent on the grasses and debris surrounding the bases of the rice plants.

The eggs.

Under natural conditions, eggs are laid in two to four rows but predominantly in two rows with two to eight eggs per row. The incidence of seven eggs to a row is most frequent. Eggs in the mass are contiguous. The eggs in a row are in a straight line and alternate with those in the next row (Pl. XV, fig. 2). The structure of the eggs has been described by de Alwis (1941). The number of eggs per mass collected in the field usually does not exceed 14 to 15. In 22 out of 25 egg-masses the eggs were laid in two rows and in 17 of these each row contained seven eggs. More than four rows were not recorded, and the number of eggs per mass varied from 8 to 15. However when egg-laying occurred under artificial conditions such as when bugs were held in any container, marked differences were noted. Under such conditions both the number of eggs in a row and the total number of eggs in each mass showed a considerable increase. The number of rows in 25 egg-masses varied between two and eight, and the number of eggs per mass from 6 to 31. Females of *S. lurida* usually lay two to three egg-masses in a period of about two weeks and die within about seven days of laying the last egg-mass.

Eggs when freshly laid show a marked variation in colour, ranging from yellow to pink, orange, grey, blue-grey and light brown. As the eggs develop they change to a deep orange-red colour when the compound eyes, egg-burster and other structures of the nymph could be observed through the chorion. At a relative humidity of 75 per cent. and a temperature of 25–28°C. the average duration of the incubation period of 25 egg-masses was 6 days (4–7).

Humidity and hatching.

Freshly laid eggs of *S. lurida* were maintained at a constant temperature of 25°C. and at a series of relative humidities ranging from 22 to 92 per cent. The results of this study are given in Table III. Development at the lower humidities (22%) was brief and ended with the eggs losing shape and becoming desiccated. At relative humidities between 43 and 64 per cent., embryonic development proceeded up to the point where fully formed nymphs could be seen through the

chorion but hatching never took place. At relative humidities of 75 per cent. and above, embryonic development and hatching proceeded normally.

The immature stages.

The structural details of the immature stages of *S. lurida* have been described by de Alwis (1941). On the seedling crop, the first-instar nymphs remain gregariously near the egg-mass for about 24 to 48 hours (Pl. XV, fig. 2) and then gradually disperse towards the lower regions of the stem of the rice plants. When freshly hatched, the nymphs can be observed to be attempting to feed on the leaves or leaf sheaths. Nymphal life is spent almost entirely on the leaf sheaths at the lower regions of the rice plants if water is present in the tracts, or, on the soil, low grasses, debris around the rice plants and at the bases of rice plants if no water is present in the rice tracts. At a relative humidity of 75 per cent. and a temperature of 25–28°C., the average duration of the instars over 25 examples was first, 5 days; second, 9 (7–11); third, 7 (5–10); fourth, 9 (7–11) and fifth instar, 12 days (11–13).

TABLE III.

Effect of relative humidity on hatching of eggs of *S. lurida* at a constant temperature of 25°C.

No. of eggs	Relative humidity (%)	Number hatched	Other observations
33	22	0	Eggs lost shape, desiccated
42	43	0	Embryos developed within eggs
55	64	0	Embryos developed within eggs
94	75	72	Development and hatching normal
25	86	80	Development and hatching normal
52	92	86	Development and hatching normal

Number of generations per annum.

The relationship of the life-cycle and generations of *S. lurida* to the rice-growing seasons and off-seasons is fairly clear-cut. In the Southern Province the first sowing of the rice crop for the year is done in April and May. Bugs migrate on to the seedling crop from their aestivation sites when the crop is about two to three weeks old. Copulation and oviposition, which commence in mid-May on the rice seedlings, continue until the end of July, and the aestivating population that had originally invaded the crop dies during this period after egg-laying. The nymphs emerging from these eggs commence to mature in early July on the crop which is in the advanced shooting or flowering stage. A small number of bugs of this generation, which represents the first complete generation on the rice crop, reach sexual maturity and are responsible for a small amount of egg-laying commencing in mid-August and ending in mid-September when harvesting commences. The remainder that mature into adult bugs later, start migration to their aestivation sites from the crop during harvest. The nymphs hatched out from the small amount of egg-laying represent a partial second generation on the crop. These nymphs continue development on the scanty supply of wild grasses in the harvested rice tracts, which are in process of desiccation, and then migrate,

in the fourth and fifth instars, to the aestivation sites where they gradually reach the adult stage with the advance of aestivation. These adults of the second generation, together with those from the first generation, proceed in due course to invade the second crop, in which the sequence of events follows a similar course to that described for the first crop.

There are, therefore, four overlapping generations in a full year. The first generation and part of the second is produced on the first crop and the remainder of the second, the third and part of a fourth on the second crop. Two overlapping generations are in aestivation at each period intervening between crops.

Aestivation of *S. lurida*.

The commencement of migration of adults of *S. lurida* to aestivation sites is dependent upon the degree of moisture and shade obtaining within the rice tracts. If dry conditions prevail, the stubble will be short and erect and the soil at the base of the rice plants will have begun to dry and cake and the bugs will migrate to the bunds of the rice-fields and neighbouring higher ground, which form the chief aestivation sites. If, on the other hand, moisture in any quantity is present in the rice tracts, and the stubble is that of lodged rice plants providing damp and shaded conditions, bug populations in all stages of development remain in the rice tracts even after harvest and migrate to other sites when the tracts are completely dried. Once the migration has been completed, however, the bugs do not seek out areas of higher moisture content for aestivation.

Adult bugs are rarely noticed on the wing at the end of each rice crop. This fact when considered together with the pattern of distribution of the bugs in their aestivation sites strongly indicates that migration to these sites by the adults is mainly achieved by walking. Bunds in the rice tracts invariably harbour the largest populations of aestivating bugs. On the rice tracts as such, bugs are found under masses of rice stubble or within the cracks of caked and dried rice-field soil. On bunds, the bugs are located within cracks of the dried soil or merely at the bases of dried grasses among the débris. The other important aestivation sites are patches of higher ground surrounded by rice tracts, high ground bordering rice tracts and on the edges of channels or waterways containing water or otherwise. On the higher ground surrounded by rice tracts, bugs are especially concentrated on the area nearer the rice tracts (Table II), and on such ground the bugs are found chiefly in the débris at the base of grasses and other plants. In this situation the bugs are also frequently found, though in very small numbers, under the dried leaf-sheaths of banana plants or in the crowns of young coconut palms. The edges of waterways are not a particularly favoured aestivation site (Table II), and bug populations are present in these sites only at the ends of seasons of very heavy bug incidence. All aestivation sites mentioned are not necessarily situations having obvious moist conditions. On the contrary, most of the aestivation sites are usually completely desiccated but invariably they give protection against sunlight.

Tracts with a few inches of dried mud followed by a sandy soil below, which do not desiccate easily to produce deep cracks, only apparently harbour more aestivating bugs than those dried muddy tracts which desiccate rapidly at the end of the season and crack deeply at that stage. The results of a survey of bug populations easily accessible in two sites of the types mentioned are given in Table IV. It was impossible to assess bug populations within the deep cracks of the highly desiccated rice tracts. However, bugs have been traced up to a depth of 2 ft. within such cracks in caked up and desiccated fallow rice tracts. That such tracts actually harbour large bug populations can be seen from the data in Table IV, which also deals with bug incidence in the same tracts after the rains and when water was introduced preparatory to tillage.

Behaviour of S. lurida in the aestivating and active stages.

Bugs in the aestivation sites are predominantly in the adult stage. Some nymphs are also present (Table II) but this is only true at the commencement of aestivation and they are mainly in the fourth and fifth instars. Development of these nymphal stages into adult bugs was observed to proceed in the aestivation sites, so that, with the advance of aestivation, almost all the bugs observed were in the adult stage.

TABLE IV.

Bug populations in two areas of differing soil type assessed during the same two consecutive seasons.

Site	Bug population per sq. yd.*			
	Tract in fallow period moist On tract with about 6 in. dried mud below which sandy soil in fallow period		Tract in fallow period desiccated On tract with over 2.5 ft. dried mud deeply cracked in fallow period	
	When fields were fallow	When water introduced to tracts preparatory to tillage	When fields were fallow	When water introduced to tracts preparatory to tillage
Rice tracts	11	1.5	0	6.5
Bunds	27	2	0.5	9
Up to 8 ft. from edge of higher ground surrounded by rice tracts	16	6	1	12.5
At centre of patches of higher ground surrounded by rice tracts	1.5	2	0	15
On other higher ground ..	2	2	0	3.5
On edges of channels and other waterways	0.25	25.5	0	19
On irrigation reservations ..	3	4	0	7
Under shrubs, etc., on road edges	0	2	0	4

* Average of 4 readings in each case.

Aestivating bugs are gregarious in habit, being found at least in pairs close to each other in the aestivation sites; this is especially so in patches of higher ground. In the rice-field bunds or in other situations, such as near banana clumps, bugs are present in larger groupings (Table V).

The feeding activity of adults fluctuates widely according to the season. Bugs in the active phases, when the crop is in the field, feed almost continuously and are responsible for various lesions, and even more drastic effects on the crop, which will be described later. Furthermore, bugs in the active phase have an abundant supply of growing food-plants such as rice and wild grasses. Feeding during this stage takes place at all hours of the day and night.

TABLE V.

Numbers and sex of bugs in groups found in various sites during aestivation.

Site	Average no. bugs per group, and range	Average no. bugs of each sex per group, and range	
		Male	Female
At base of banana clumps on higher ground (5 groups of bugs)	9.8 (6-16)	5 (3-7)	4.8 (2-8)
At base of coconut palms on higher ground (2 groups)	2.5 (2-3)	1	1.5 (1-2)
At base of weeds on higher ground (21 groups)	2.9 (1-6)	1.6 (0-4)	1.3 (0-3)
On bunds (6 groups)	12 (5-21)	6 (2-12)	6 (3-11)

Aestivating bugs have not been observed feeding under natural conditions during the day-time but remain relatively motionless in the aestivation sites. At dusk a few bugs have been noted to insert their stylets into withering grasses in their environment and withdraw them after a short period, and some activity was apparent when bugs performed limited walking in their aestivation sites but they

TABLE VI.

Survival of adults of *S. lurida* under various conditions of food sources and relative humidity.

Environmental conditions	Duration of exposure to conditions	Percentage survival
On rice plants	30 days	96
	60 "	80
On cotton lint moistened with water	30 "	96
	60 "	70
No substratum—at room temperature and 60% R.H. ..	24 hr.	0
No substratum—at room temperature and 70% R.H. ..	24 "	12
No substratum—at room temperature and 78% R.H. ..	24 "	90
	48 "	62
	72 "	0
No substratum—at room temperature and 87% R.H. ..	24 "	100
	48 "	100
	72 "	80
	96 "	2

TABLE VII.
Effect of exposure of adults of *S. lurida* to a humidity gradient.

Time of observation (bugs introduced at 10.30 a.m. or 4.30 p.m.)	Distribution of 40 bugs introduced at lowest humidity chamber at 10.30 a.m. or 4.30 p.m.										Distribution of 40 bugs introduced at highest humidity chamber at 10.30 a.m. or 4.30 p.m.									
	Relative humidity (%)										Relative humidity (%)									
	7	19	25	43	47	74	87	92			7	19	25	43	47	74	87	92		
10.30 a.m.	40	0	0	0	0	0	0	0			0	0	0	0	0	0	0	40		
11.30 a.m.	22	10	2	3	0	3	0	0			0	0	0	0	0	0	0	40		
12.30 p.m.	21	9	1	3	3	3	0	0			0	0	0	0	0	0	0	40		
1.30 p.m.	21	9	1	2	2	5	0	0			0	0	0	0	0	0	0	40		
2.30 p.m.	21	8	2	0	5	3	0	1			0	0	0	0	0	0	0	40		
3.30 p.m.	16	7	2	2	5	6	0	2			0	0	0	0	0	0	0	40		
4.30 p.m.	14	11	4	0	2	5	0	4			0	0	0	0	0	0	0	40		
5.30 p.m.	5	4	0	0	4	5	3	19			0	0	0	0	0	2	3	35		
6.30 p.m.	7	1	2	1	7	4	3	15			2	1	3	0	3	2	2	27		
7.30 p.m.	6	0	0	1	2	7	5	19			5	2	3	2	2	3	2	21		
8.30 p.m.	5	0	3	3	2	5	4	18			5	3	0	1	2	5	7	17		
9.30 p.m.	5	2	0	0	0	4	7	22			6	1	0	0	1	4	2	26		
4.30 p.m.	40	0	0	0	0	0	0	0			0	0	0	0	0	0	0	40		
5.30 p.m.	10	4	2	2	5	1	5	11			1	0	0	0	0	0	10	29		
6.30 p.m.	2	2	0	0	2	4	5	25			2	5	3	3	2	5	6	14		
7.30 p.m.	1	1	0	3	2	5	7	21			5	4	2	2	1	1	7	18		
8.30 p.m.	1	2	1	1	1	9	3	22			0	0	1	0	1	4	4	30		
9.30 p.m.	5	0	1	1	1	3	3	26			1	0	1	0	1	2	4	31		

rarely took wing. Feeding of aestivating bugs under field conditions, therefore, is very restricted.

The condition of the alimentary tract and the reproductive organs of aestivating adults was examined by dissection. Little or no food material was present in their guts when compared to those of bugs in the active condition when the crop is present; in the latter case, the alimentary tracts were consistently dilated with food material. The reproductive organs were underdeveloped and represented the condition apparent in sexually immature adults in the active stage. The relatively empty alimentary tracts and the retarded condition of the internal reproductive organs continued until the first rains and migration to the seedling rice crop began.

Laboratory tests have been conducted to evaluate the importance of food and moisture in the survival of freshly emerged adults under caged laboratory conditions. Bugs were either maintained on rice plants or on plugs of cotton lint moistened with water, or without any food or material from which moisture could be imbibed, kept under a series of relative humidities ranging from 60 to 90 per cent. The adult bugs used in these tests were about 3 days old, and the results are given in Table VI. Survival was best, as would be expected, where the rice plant was available, but good survival was also noted with water alone. Under moist conditions alone, without any food, survival was poor. Aestivating bugs gave similar results when subjected to the same test conditions.

The response of adults to moisture was studied by using a simplified apparatus, illustrated in Plate XV, fig. 3. This consisted of an elongated chamber 21 in. long, 4 in. wide and 0.75 in. deep, with a closely fitted lid. The chamber was divided into eight equal sections. The bottom of each section carried a fine-mesh (80 gauge) trough 1.5 in. square and 0.5 in. deep. There was a circular opening of 0.5 in. diameter at one end of the cover. This opening could be tightly closed with a cork. The chamber was prepared for use by placing it on top of a series of eight staining jars each carrying a saturated solution of a particular salt. Each of the eight mesh troughs rested within the top of one staining jar and the liquid surface in a jar was about 0.1 in. below the mesh. The solutions in the jars were selected to give a humidity range from 11 to 92 per cent. at 25°C., and the jars were so arranged as to give a humidity gradient from one compartment to the next. The results of these studies are given in Table VII. The pattern of response of both active and aestivating bugs to a moisture gradient was the same. The humidity reaction of bugs placed under conditions of very low humidity was sharper after dusk than during day-time. Bugs placed under high humidity conditions remained undisturbed until dusk, when small-scale wandering, apparently in search of food, began. There was no difference between the humidity reactions of aestivating and active adults.

Damage to rice plants caused by feeding of *S. lurida*.

Field observations.

Damage to the rice crop by *S. lurida* in the field can be classified into four categories, viz., (a) highly localised and clearly demarcated light- to deep-brown lesions on leaves, (b) more extensive chlorotic markings on leaves, (c) death of central shoot or portions of central shoot, (d) death of entire plants.

Localised leaf lesions caused by direct feeding of *S. lurida* upon the leaves of rice plants result initially in the production of water-soaked areas around the point of insertion of the oral stylets. With time, these areas turn brown, usually darker brown at the margins, and wither and at this stage they strongly resemble those caused by the fungus disease, *Piricularia oryzae*. As these lesions age in the field they become bleached into a creamish to very light-brown colour. Lesions of this description (Pl. XVI, fig. 1, A & B) are found mainly on seedling rice and

TABLE VIII.
Effects of feeding of various numbers of adults of *S. lurida* for varying periods of time upon three-week-old rice seedlings.

Location of caged bugs	No. of bugs per plant	Duration of exposure (hr.) of plants to bugs	Observations on plants after infestation with bugs									
			1 day later	2 days later	4 days later	7 days later	14 days later					
			Original central shoot	Other leaves	Original central shoot	Original central shoot	New central shoot	Main stem	No. of tillers	Original plant	Original central shoot	New shoot
Parts of stem above 1.5 in. from growing point	1	24	Flaccid	1-1S* 2-N	Chlorotic	Tip dried	Chlorotic	Normal	2	Normal	Tip dried	Normal
	1	48	Flaccid	3N	Chlorotic	Tip dried	Normal	Normal	1	Normal	Tip dried	Normal
	1	72	Rolled	1-1S 2N	Chlorotic	Tip dried	Normal	Normal	1	Normal	Tip dried	Normal
	1	96	Rolled	2-2F 1N	Dried	Dried	Chlorotic	Necrotic	2	Necrotic	Dried	Tip dried
	2	24	Rolled	2-2S 1N	Chlorotic	Tip dried	Normal	Normal	2	Normal	Tip dried	Normal
	2	48	Rolled	1-1S 2N	Chlorotic	Tip dried	Normal	Necrotic	2	Normal	Tip dried	Normal
	2	72	Flaccid	2-2S 1N	Chlorotic	Dried	None	Necrotic	2	Dried	Dried	None
	2	96	Rolled	3N	Dried	Dried	None	Necrotic	5	Dried	Dried	Chlorotic
	3	24	Rolled	3-4S	Dried	Dried	None	Necrotic	1	Dried	Dried	None
	3	48	Rolled	3-4S	Dried	Dried	None	Necrotic	3	Dried	Dried	None
	3	72	Rolled	3-8S	Dried	Dried	None	Necrotic	3	Dried	Dried	None
	3	96	Rolled	3-6D	Dried	Dried	Chlorotic	Necrotic	3	Necrotic	Dried	Tip dried
	4	24	Rolled	3-7D	Dried	Dried	None	Necrotic	4	Necrotic	Dried	None
	4	48	Rolled	3-10D	Dried	Dried	None	Necrotic	5	Dried	Dried	None
	4	72	Rolled	3-9D	Dried	Dried	None	Necrotic	4	Necrotic	Dried	Tip dried
	4	96	Rolled	3-7D	Dried	Dried	None	Necrotic	2	Necrotic	Dried	None
At and up to 1.5 in. from growing point	1, 2, 3 and 4 bugs, each for 24, 48, 72 and 96 hr.		Rolled	3-3 to 10D	Dried	Dried	None	Necrotic or dried	None	Dried	Dried	None
	Check		Normal	Normal	Normal	Normal	Normal	Normal	Normal	Normal	Normal	Normal

Three plants were used for test feeding.

N = normal, S = snapped, F = flaccid, D = dried.

* First figure = number of plants affected; second figure = number of leaves affected in the plants.

rarely on maturing rice plants and are strongly reminiscent of those caused by MIRIDAE of the genera *Helopeltis*, *Sahlbergella* and *Distantiella* on the cacao plant (J. Nicol, ?1947 (The insect pests of cacao trees.—Typescript report, W. Afr. Cacao Res. Inst., Tafo); Carter, 1952; Fernando & Manickavasagar, 1956).

Chlorotic lesions are chiefly observed on seedling rice in the pre-shooting stage. It is the commonest observable type of damage associated with attack in the field. The lesions are white in colour without clearly demarcated margins. The white areas gradually diffuse into the green of the healthy portions of the leaf. These lesions are extremely variable in size and location. When they first appear they are as turgid as the rest of the leaf but they soon lose their turgidity, wither, turn light brown and gradually dry up, resulting frequently also in death of portions of the leaf beyond the lesions (Pl. XVI, fig. 1, C).

Death of the central shoot is chiefly observed in rice plants in the pre-shooting stage in the field. The central shoot is either rolled up longitudinally and wilted, or completely dried.

Death of entire plants is noticed only in seedling rice up to about six weeks old in the field during seasons of heavy attack.

Laboratory observations.

Experiments under controlled laboratory conditions were next conducted with a view to elucidating the conditions under which the various responses of the rice plant to feeding, observed in the field, occurred. Feeding tests were carried out with adults in the active phase both on seedling and on maturing rice plants.

The first series of tests aimed at investigating the possibility that a toxin, which would eventually become systemic in its action, was involved in the feeding damage caused by this pest. Adults were enclosed on two of the well-developed leaves of each of three 4-week-old rice seedlings at the rate of two bugs per plant and four bugs per plant. Feeding was permitted for 48 hours, and observations were maintained on the development of lesions and on the effect of the feeding on the growth of the plants.

The first reaction was apparent within two hours of commencement of the test; parts of the leaves which had been fed upon lost their turgidity and the tissues appeared collapsed. In normal sunlight these areas turned brown and their margins were clearly demarcated from the rest of the green leaf by a fringe of deep brown. These lesions strongly resembled those caused by the fungus disease, *Piricularia oryzae*, on rice. Leaf tissues which had been fed upon usually reached this stage within 24 hours of commencement of feeding. These necrotic patches dried up completely within about two days and in about one week had become bleached into a very light-brown colour (Pl. XVI, fig. 1, A & B). Whilst these changes were taking place on the portions of the leaves exposed to direct feeding by the bugs the rest of the seedlings grew normally. No difference could be noted on the growth rates of the test seedlings over a period of two weeks, when compared with plants not exposed to feeding.

In the next series of tests, adults were caged on the stem either above 1.5 in. from the growing point (which is located at the base of the seedling) or at and up to 1.5 in. from the growing point of 3-week-old rice seedlings. The details of these tests, summarising the results obtained from plants for each infestation rate and test period of exposure of plants to bugs, are given in Table VIII. These data indicate that the first reaction of the seedling to feeding by the bugs, whether near the growing point or above 1.5 in. from it, is the wilting of the central shoot followed by a longitudinal rolling up of this shoot. The term central shoot is used here to connote the youngest leaf which was emerging at the time the feeding tests were started. The speed of this response was related to the number of bugs feeding on the stem and the location of the feeding. Feeding near the growing

point evoked the wilting of the central shoot more rapidly than feeding on the upper regions of the stem.

Within two days of the test feeding by the bugs the older leaves showed a response to the attack. Leaves either lost their normal turgidity and snapped along the midribs, or had wilted completely and dried. This reaction of the rice seedlings was also proportional to the number of bugs feeding, the duration of the feeding and the location of the feeding. Here again the reaction was more drastic where feeding on the stem was allowed near the growing point.

The central shoot invariably wilted, rolled up and gradually dried within two days in all cases where two bugs were allowed to feed for 96 hours or three or more bugs were allowed to feed for 24 hours or more, regardless of the location of the feeding on the stem. In all those cases of one bug feeding for 24 to 96 hours or two bugs feeding for 24 to 48 hours on regions of the stem above 1.5 in. from the growing point, death of the central shoot was not complete. That portion of the growing shoot which had emerged at the time of feeding wilted and eventually dried up. The portion of the growing shoot which emerged subsequently appeared healthy on emergence but exhibited chlorosis in patches. When fully emerged, such leaves showed the typical leaf-tip death. The chlorotic patches varied in size and location. These patches were pure white in the centre but gradually diffused into the green of the rest of the leaf (Pl. XVI, fig. 1, C). Such chlorotic patches withered within about 48 hours after emergence and opening of the young leaf and if they extended over a transverse section of the leaf that portion of the leaf beyond the chlorotic patch also wilted and dried. The subsequent new shoot occasionally also showed chlorotic patches.

Another consequence of feeding by *S. lurida* on rice seedlings is the killing of the main axis of the plant unless only light feeding on the regions above 1.5 in. from the growing point was permitted. In those plants where feeding was allowed above 1.5 in. from the growing point, death of the main axis resulted where two bugs fed for 72 hours or three or more bugs fed for 24 hours or more. However, in all cases of such feeding, death of the plant was not complete because tillering was vigorous within 14 days. On the other hand, where bugs fed around the growing point, death of the plant, which occurred in all cases, was complete, and no tillering occurred.

In the next series of tests, adults were allowed to feed either at the base or at or around and above the growing point of rice plants 2½ months old, which had passed the shooting stage. In such plants the growing point was about 6 in. or more above the base of the plants. Bugs were enclosed at the rate of three per plant to feed upon one of the regions of the stem, viz., at the base, at the growing point or 3 in. above the growing point. Each of the regions exposed to the bugs extended over about 3 in. of stem length. Feeding at the base had to be continuous for 21 days before the plant showed the first reaction of wilting and subsequent drying up. Sectioning of the base of the stems of such plants showed that concentrated mechanical injury caused by the penetrating stylets of the bugs during feeding had caused their death. Where feeding was permitted at the growing point, death of the central shoot occurred within three days of feeding and the entire plant had dried on the twelfth day after feeding. Where feeding occurred above the growing points, the effects were similar to that obtained with light feeding in the same region of seedling rice plants, in that chlorotic patches developed on the new leaves after the bugs were withdrawn.

Parasites and predators.

S. lurida has no recorded predators in Ceylon either in its immature or adult stages, but attack on the eggs by a Hymenopterous parasite is extensive. What appears to be a low mortality of the adults caused by entomogenous fungi, particularly during aestivation, has also been observed.

The egg-parasite is the minute Scelionid, *Telenomus triptus* Nixon. This parasite is extremely active in the field when the bugs are ovipositing and during parasitisation of egg-masses it is extremely tenacious and cannot be dislodged even by violent movement of the egg-mass (Pl. XVI, fig. 2). Parasitisation of eggs under field conditions fluctuated between 30 and 36 per cent. as assessed from recorded observations between the years 1953 and 1955.

Under laboratory conditions, the parasitisation of eggs by *T. triptus* was observed closely. One- to ten-day-old parasites were used, and the results of these studies are given in Table IX. The parasites, on being provided with a leaf carrying an egg-mass, rapidly located it and then proceeded to examine it closely with their antennae in rapid motion. Only those eggs which had not been previously parasitised were used by the parasite for oviposition. Oviposition in a fresh egg-mass was not effected in an orderly fashion but in no instance was a parasite observed to oviposit or even attempt oviposition more than once in a single host egg. The ovipositor is inserted either into the egg cap or into the side of the egg. The time taken for each oviposition was highly constant at 1 minute 45 seconds, and 3 to 5 seconds later the next commenced. Eggs that had been successfully parasitised turned deep purplish-black in colour on about the third day later. As can be seen from Table IX, parasites maintained on sugar solution, and 1 to 10 days old, can successfully parasitise host eggs under laboratory conditions. Host eggs, which normally hatch in six days, were susceptible to successful parasitisation by *T. triptus* under laboratory conditions even up to the fifth day of their development when the fully developed nymphs could be observed through the chorion. However, 5-day-old eggs more frequently produced nymphs than parasites if attacked by *T. triptus*. On an average, parasites emerged from the host egg from 12–15 days after oviposition. Parasitised eggs on emergence of the parasites had irregular apertures on the operculum and a blackish residue within. *T. triptus* lived from 8 to 22 days after emergence if maintained on sugar syrup.

During aestivation and in the following preoviposition period *S. lurida* is susceptible to attack by fungi (Pl. XVI, fig. 3). If diseased, the insects appear sluggish and die shortly afterwards, and 24–48 hours later fructifications of a fungus appear. Two fungi recovered from affected bugs are *Metarrhizium anisopliae* and *Penicillium citrinum*. The former is normally responsible for the green muscardine disease in insects but the latter has to date not been recorded as being entomogenous.

Discussion.

A study of the Japanese literature on *S. lurida*, especially the work of Katsumata (1929) and Kawasi (1955), shows many interesting similarities and also differences in behaviour between *S. lurida* in Japan and in Ceylon.

In Japan, *S. lurida* develops one generation per year and the first generation of bugs developed on the rice crop hibernates in the winter in the adult state, to invade the next year's crop in the seedling stage. In Ceylon, on the other hand, the pest develops 3 to 4 generations per year on the two rice crops and aestivates as an adult during the two fallow periods. These differences are, however, related to radical differences in the climates obtaining in the two countries.

In Japan, *S. lurida* feeds both as an adult and in the nymphal stages on all parts of the rice plant, whether seedling, maturing or mature. In Ceylon, this insect feeds as an adult on all parts of the seedling and only on the basal region of maturing or mature rice plants, while in the nymphs, feeding is limited to the basal parts of the rice plants whether seedlings or otherwise. The difference in the feeding habits of this insect in Japan and Ceylon results in differences in the incidence and distribution of their feeding lesions on the rice plants in the two countries.

TABLE IX.
Parasitisation of eggs of *S. lurida* by *Telenomus triptus*.

No. of egg-masses introduced	No. of eggs in masses	Age of eggs (days)	No. of parasites to which eggs exposed	Age of parasites (days)	Period for parasites to emerge (days)	No. of parasites emerged	No. of nymphs emerged	Recent parasitisation (%)
3	70	1	1	1	11-13	67	—	95
4	16	1	1	3	15	15	—	93
1	10	1	1	9	12	10	—	100
9	100	1	1	10	—	—	100	—
1	14	1	2	2	12	14	—	100
1	14	1	2	2	15	14	—	100
1	25	1	2	2	12-15	24	—	96
1	28	1	2	2	13-15	28	—	100
1	22	2	2	2	12-13	20	—	99
1	27	2	2	2	13-15	27	—	100
2	40	3	2	2	13-15	34	—	85
1	27	4	2	2	13-15	27	—	100
1	29	5	2	2	12	12	—	42
1	8	5	1	1	—	—	8	—
1	31	5	2	2	14-16	31	—	100
1	15	5	1	9	—	—	15	—
1	24	5	1	9	—	—	24	—

It would appear that, when the bugs feed upon the stems of rice plants, a toxin which either diffuses upwards or a toxin with localised action but which affects the translocation of water is involved. The latter appears to be more likely as can be seen from the further effects of feeding by *S. lurida*. This type of damage is similar to that caused by the Pentatomid bug, *Chlorochroa sayi* (Stål), on potato plants in the U.S.A., where the first symptom is the wilting of the leaves (Daniels, 1939).

Very frequently the stylet tract of the feeding bug is noticeable in the centre of the extensive white lesions (see p. 571) that develop subsequent to feeding. The extent of these lesions most likely defines the limits of the diffusion of a toxic component in the salivary secretion which has as one of its properties the inhibition of the development of chlorophyll. The fact that only feeding near the growing point always leads to the complete death of the plant without subsequent tillering is a further indication that the salivary toxin is not one which becomes fully systemic in its action but diffuses only over a limited area from the point at which the stylets were inserted.

In addition to the various reactions in the rice plant to feeding by *S. lurida* noted in Ceylon, Kawasi (1955) has recorded the development of sterile branches from the higher nodes in attacked rice plants in Japan. This phenomenon of upper nodal branching is usually recorded in Japan as being a result of exposure to extreme physiological stress such as to frost. This type of branching never occurs in Ceylon and is more likely to be the consequence of physiological differences between the Japonica and Indica varieties of rice grown in the two countries rather than of physiological difference between the strains of *S. lurida* in Ceylon and Japan.

Summary.

The black rice bug, *Scotinophara lurida* (Burm.), is widely distributed in Ceylon in areas where rice is grown under irrigation. It first became a serious pest in 1940 and, periodically since, it has assumed epidemic proportions in the Southern Province where two crops of rice are grown annually. Each crop takes from $3\frac{1}{2}$ to 4 months to mature, the fields lying fallow in the intervening periods. During these periods the insects aestivate, in the adult or late nymphal stages, in cracks in the bunds in the rice-fields or on neighbouring higher ground. They remain motionless for the most part during aestivation, are gregarious and occur as much as 2 ft. below ground-level.

The adults leave the aestivation sites in April and May and settle in the first crop when it is two to three weeks old, and a subsequent aestivating population behaves similarly in November and December for the second crop. There is at first considerable flight activity at dusk, and at night, and after feeding for about a week on the rice seedlings copulation takes place and oviposition commences about ten days later.

Egg-masses in the field usually consist of two rows, each containing seven eggs, but under artificial conditions the number of eggs and rows were considerably in excess of these figures. At a relative humidity of 75 per cent. and temperature of 25–28°C. in the laboratory, the average duration of the stages was: egg, 6 days; the five instars, 1st, 5; 2nd, 9; 3rd, 7; 4th, 9 and 5th, 12 days, respectively.

There are four overlapping generations during the year. The first generation, and part of the second, is produced on the first crop and the remainder of the second, the third and a part of a fourth generation on the second crop. The periods intervening between the two crops are passed in aestivation by the nymphal or adult stages of two overlapping generations.

Damage to the rice crop in the field consists of localised leaf lesions, chlorotic lesions, which gradually dry up and frequently result in the death of that portion of the leaf between the lesion and the leaf tip, death of the central shoot or death

of the entire plant. Laboratory experiments showed that feeding near the growing point of a seedling always leads to death of the plant without subsequent tillering but, when feeding took place more than 1.5 inches above the growing point, the leaves developed necrotic patches and dried off but the plant tillered and the rest of it grew normally. The nature of the chlorotic areas surrounding the initial lesions, it is suggested, may be due to the diffusion of a toxic compound in the salivary secretion of the insect.

No predators of *S. lurida* have been recorded in Ceylon but the eggs are parasitised by *Telenomus triptus* Nixon and parasitisation in the field was assessed as between 30 and 36 per cent. in the years 1953 to 1955. The parasite only lays one egg in a single host egg. Details are given of the course of parasitisation under laboratory conditions.

S. lurida is a major pest of rice in China and Japan and the behaviour of the pest in these countries is compared with that in Ceylon.

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References.

- DE ALWIS, E. (1941). The paddy Pentatomid bug *Scotinophara* (*Podops*) *lurida* Burm.—*Trop. Agriculturist* **96** pp. 217–220.
- CARTER, Walter (1952). Injuries to plants caused by insect toxins. II.—*Bot. Rev.* **18** pp. 680–721.
- DANIELS, L. B. (1939). Appearance of a new potato disease in northeastern Colorado.—*Science* **90** p. 273.
- FERNANDO, H. E. (1960). The susceptibility of the rice Pentatomid bug, *Scotinophara lurida* (Burm.), to insecticides, and the insecticidal control of this pest in Ceylon.—*Bull. ent. Res.* **50** pp. 717–735.
- FERNANDO, H. E. & MANICKAVASAGAR, P. (1956). Economic damage and control of the cacao Capsid, *Helopeltis* sp. (fam. Capsidae, ord. Hemiptera) in Ceylon.—*Trop. Agriculturist* **112** pp. 25–36.
- KATSUMATA, K. (1929). Studies on the rice black bug *S. lurida*.—*Ishikawa Pref. agric. Exp. Sta. Rep.* 1929.
- KAWADA, A., KATO, S., MUKOO, H. & FUKUNAGA, K. (1954). Insects and diseases of rice plants in Japan.—*Nat. Inst. agric. Sci., Tokyo*.
- KAWASI, E. (1955). Research items on the rice Pentatomid bug, *Scotinophara lurida* Burm.—*Ishikawa Pref. agric. Exp. Sta. Rep.* 1955.



FIG. 1. Adult of *Scotinophara lurida* on rice leaf ($\times 6$, approx.).

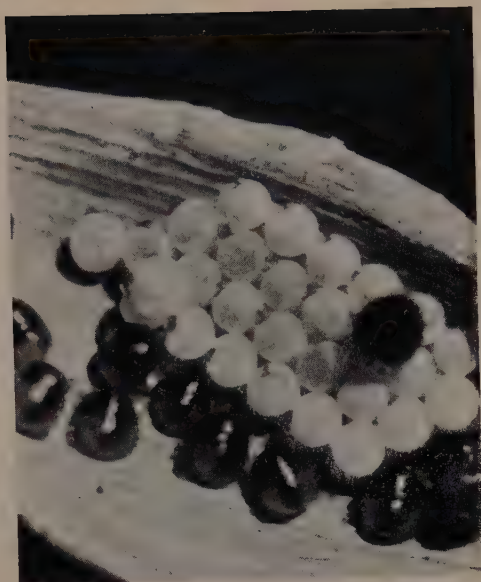


FIG. 2. Freshly hatched nymphs of *S. lurida* near egg-mass. The egg-bursters can be seen below the open opercula of the hatched eggs ($\times 10$, approx.).



FIG. 3. Equipment used for the study of the reactions of adults of *S. lurida* to a humidity gradient.

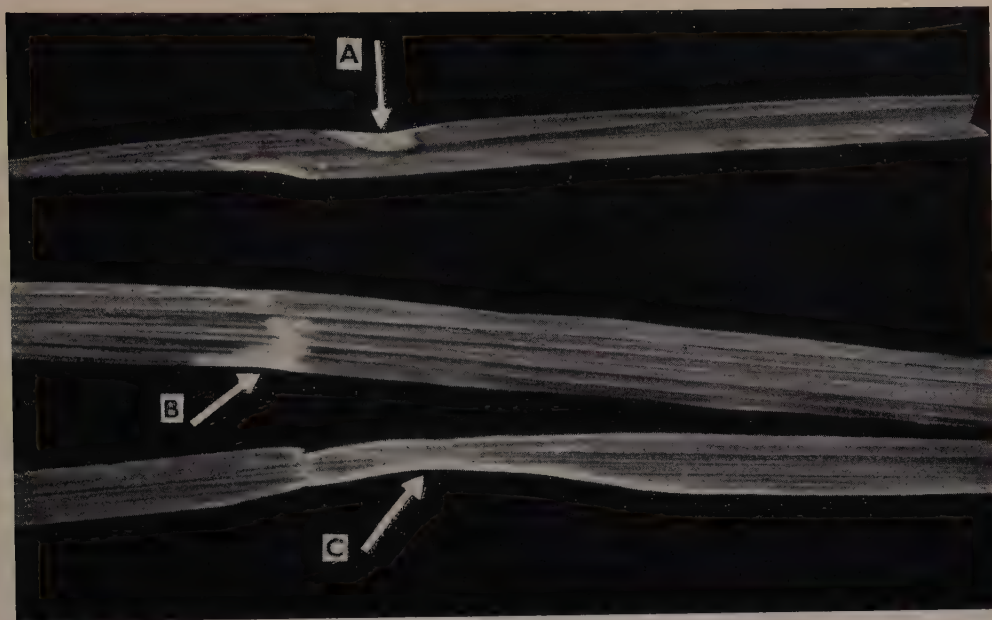


FIG. 1. Various types of lesions caused by feeding of *Scotinophara lurida* on rice plants. A, B, localised lesions caused directly by feeding; C, chlorotic lesion.



FIG. 2. *Telenomus triptus* ovipositing in eggs of *S. lurida* ($\times 20$, approx.)



FIG. 3. Adult of *S. lurida* killed by the fungus, *Metarrhizium anisopliae*.

THE CONTROL OF YELLOW TEA MITE, *HEMITARSONEMUS LATUS* (BANKS), WITH DDT ON COTTON IN UGANDA.

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E.M.N

The yellow tea mite, *Hemitarsonemus latus* (Banks), is distributed throughout the tropics and is also known as a greenhouse pest in temperate regions. It has been recorded as damaging cotton, and also tea, rubber, castor, *Citrus*, *Cinchona* and many ornamental and wild shrubs. In Africa it is widespread (Pearson, 1958) and was first recognised as a pest of cotton in the Belgian Congo in 1936 (Vrydagh, 1942) where the symptoms are known as 'acariose'. Descriptions of the damage caused by this pest to the cotton plant are given by Vrydagh (1942), Micheltore (1954), Schmitz (1956) and Pearson (1958); Gadd (1946) has likewise given details of its life-history and habits.

The damage caused by *H. latus* was first observed on cotton in Uganda in 1945 in the north of Teso District. In 1950 it was seen on Serere Experiment Station, in Teso District, and it was also recorded near Kampala (Micheltore, 1954). Since then it has been seen in all the cotton-growing areas of Uganda, including small experimental cotton plots in the dry thorn-bush country of Karamoja District. It is now widespread and common but its distribution is extremely patchy, even within plots.

Control with toxicants.

Considerable work has been done in temperate regions on the control of this pest in greenhouses but this work is hardly applicable to field conditions as in most cases it concerns the use of smokes and aerosols. It is interesting to note, however, that tea mite is readily controlled by BHC smokes (Fjeldalen, 1951) but not by sprays containing schradan (Smith, Fulton & Hall, 1950).

Experimental work on cotton in the Congo (Schmitz, 1956) showed that sprays containing sulphur, toxaphene, DDT and parathion prevented infestation, and that a dust containing 10 per cent. toxaphene and 5 per cent. DDT gave good control, while one containing 2 per cent. parathion did not. In Uganda, a considerable number of trials have been carried out using BHC, DDT and toxaphene against *Earias* spp. (Lep., NOCTUIDAE) and *Lygus vosseleri* Popp. (Hem., MIRIDAE) and during the course of these trials observations on tea-mite damage were made. The bulk of this work was carried out at Serere; Micheltore (1954) suggested that DDT was giving no control here and might even be encouraging tea-mite attack, and Thomas (1956) reported that BHC sprays gave excellent control but that DDT sprays increased tea-mite damage. The records show that both insecticides were applied as wettable powders. BHC was less successful than DDT in controlling *L. vosseleri* (Watson, 1953) and so no further trials have been done with it; toxaphene was dropped because it consistently produced phytotoxic symptoms on cotton foliage, as was noted by Coaker (1956).

In experiments using McKinlay's (1954) single-line technique, tea-mite damage was rarely observed on the sprayed rows when these were treated with a DDT-toxaphene mixture or with DDT only, although it was frequently seen on the controls. The DDT formulation used in these trials was an emulsified solution and all trials since these have been carried out with a DDT miscible-liquid formulation. The standard practice in these trials—and that now used by peasant farmers—was to apply DDT at 1 lb. active ingredient per acre four times at 10-day intervals commencing nine weeks after sowing. The general impression gained

from this work was that a miscible-liquid formulation of DDT was certainly not increasing the incidence of tea-mite damage and might even be reducing it.

At Serere in 1958, isolated, unsprayed half-acre plots of cotton were found to be heavily attacked by tea mite and so counts were taken of the amount of damage on trials of sprays directed against the insect-pest complex. Counts of plants showing any sign of the characteristic leaf damage due to tea mite (see Schmitz (1956), p. 335, coloured plate) were made in samples of 100 plants. Although casual observations suggested that DDT was controlling the mite, these samples did not bear this out, there being no significant differences between sprayed and unsprayed plots. At the same time, on a small sub-station some 35 miles away, a sprayed cotton plot was completely free of tea-mite damage while an unsprayed plot showed severe leaf symptoms.

In 1959, counts of tea-mite damage were taken on several trials at Serere in which DDT was applied at 1 lb. active ingredient per acre per application. Counts were based on the number of plants showing any sign of damage in random

TABLE I.

Incidence of tea-mite damage in insecticide trials on cotton, Serere, 1959.

Trial 1, sown 15.v.1959		Trial 2, sown 22.v.1959	
4 sprays at 10-day intervals beginning	Mean no. of plants showing tea-mite damage/100 plants	Sprays beginning 8 weeks after emergence of seedlings	Mean no. of plants showing tea-mite damage/100 plants
a. 25 June ..	29.5	a. 4 at 10-day intervals	20.0
b. 15 July ..	25.5	b. 3 at 15-day intervals	37.0
c. 15 July ..	24.8	c. 2 at 20-day intervals	38.8
d. Control ..	36.8	d. Control	47.5
Significance (P) ..	N.S.	Significance (P)	< .001.
L.S.D. at .05 ..	—	L.S.D. at .05	6.6

In Trial 1, treatments b and c were sprayed at the same time, in error.

samples of 100 plants per plot on two large trials. These two trials were sown within seven days of one another in mid-May on adjacent 10-acre blocks at Serere. One of these blocks consisted of two five-acre parallel strips, while the other had four strips, each of $2\frac{1}{2}$ acres. In both blocks the strips were 35 yd. wide. Both trials had four replicates of four treatments, each plot being of half an acre, after exclusion of areas affected by termitaria, etc., and the samples were taken from the centre of these plots to try to reduce the effect of any drift of insecticide or migration of pests from plot to plot. In trial 1, the DDT was applied four times at 10-day intervals beginning at different stages in the development of the plants based on different criteria (the appearance of the first bud, eight weeks after the emergence of the seedlings, or the appearance of the first flower (but see footnote to Table I)), and although there were no significant differences between the samples, plants subjected to the later treatment, which was applied at the height of the tea-mite attack, showed less damage (see Table I). In trial 2, there were varying numbers of sprays applied, but all treatments began eight weeks after the emergence of the seedlings, and the samples showed that in each of the spray treatments there was significantly less damage than in the unsprayed control.

A third trial on which tea-mite damage counts were taken was laid down at Serere by the Empire Cotton Growing Corporation's plant breeder, to whom I am grateful for permission to use these results. This trial compared twelve plant spacings, sprayed and unsprayed, in six replicates. Four applications were made at ten-day intervals, beginning eight weeks after emergence of the seedlings. Since the individual plots were very small, only six plants were examined per plot, one plant being selected at random in each of six rows, giving a total of 36 plants per treatment. It was very apparent to the naked eye that there was much less tea-mite damage on the sprayed cotton and these differences proved highly significant in the analysis of variance. The details are given in Table II and the correlation diagram in figure 1.

TABLE II.

Incidence of tea-mite damage in sprayed and unsprayed plots on a plant spacing trial, Serere, 1959.

Spacings (ft.)	Sq. ft./ plant	Mean no. of plants per plot showing tea-mite damage		Results of analysis of variance
		Sprayed	Unsprayed	
1 × ½	½	1.5	2.5	Whole experiment : Spray v. no spray $P < .001$ Between spacings $P < .001$ Interaction spray × spacing $P < .001$
1 × 1	1	1.83	3.33	
2 × ½	1	1.67	3.67	
1 × 1½	1½	1.67	3.33	
3 × ½	1½	1.67	3.83	Sprayed plots only : Between spacings N.S.
1 × 2	2	1.83	4.33	
2 × 1	2	2.0	4.67	
2 × 1½	3	1.5	4.5	
3 × 1	3	1.83	5.33	Unsprayed plots only : Between spacings $P < .001$
2 × 2	4	2.0	4.5	
3 × 1½	4½	1.83	4.83	
3 × 2	6	1.83	4.67	

As there are no significant differences between the tea-mite damage counts in the sprayed plots, the unsprayed plots can be treated as a separate randomised block experiment. This analysis shows that the tea-mite damage is significantly heavier ($P < 0.001$) on the wider spaced cotton, the least significant difference (at $P = 0.05$) between spacings being 0.96 plants per plot.

Discussion.

Previous observations had suggested that a miscible-liquid formulation of DDT markedly reduced the amount of damage caused to the foliage of the cotton plant by *H. latus*. The results of the trials given above confirm this. Damage has been reduced, although control has never been complete; this is in contrast to the increased damage noted following the use of DDT as wettable powder.

Yield increases obtained following spraying have not been given, since in all these trials the main factors in reducing the yield were insects, their effects being measured as insect damage to flower buds, flowers and bolls. In no trials to date has a toxicant that is purely acaricidal in action been used, so that any yield increases that may have been brought about by reducing the tea-mite damage cannot be separated from those due to reducing insect damage. In the sprayed cotton, where there was very little tea-mite damage, the wider spacings gave the lowest yields, whereas in the unsprayed cotton the wider spacings, which had the highest tea-mite damage, gave the highest yield. This

suggests that tea-mite does not affect yield very greatly. Schmitz (1956) recommends wide spacing as a means of reducing tea-mite damage, but does not say what he considers to be wide spacing. In the Serere spacing trial, cotton sown at 3×1 ft. suffered the heaviest attack but all the wider spacings were fairly similar. The widest spacing in this trial was 6 sq. ft. per plant, and it is impossible to decide whether even wider spacings would have lowered the tea-mite damage counts on the unsprayed cotton. The tea-mite damage on the sprayed cotton is obviously unaffected by the plant spacing.

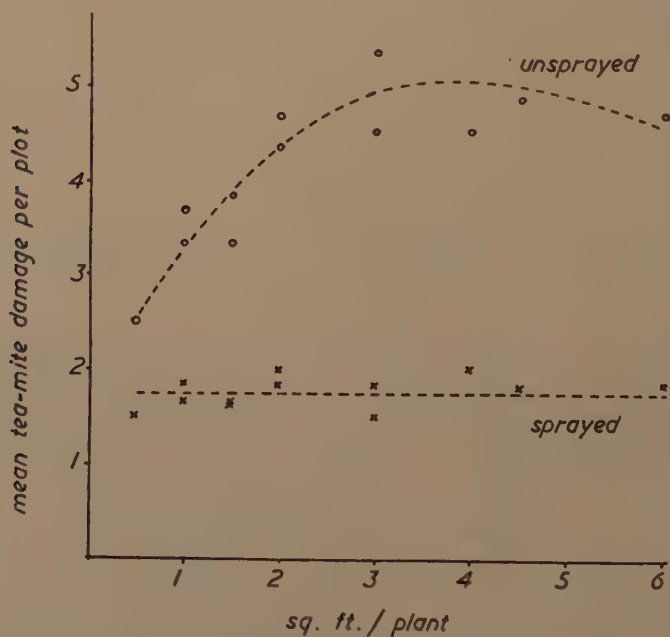


Fig. 1.—Tea-mite damage on sprayed and unsprayed cotton in relation to plant spacing.

Schmitz records that tea-mite attack can reduce yields of cotton in the Congo by 30–70 per cent., but this appears to be much greater than anything experienced to date in Uganda. In order to study the effect on yield more closely, a series of examinations was made on some unsprayed cotton plants deliberately selected for the presence, or absence, of tea-mite damage. On young cotton plants, those with obvious tea-mite damage had retained fewer buds than the undamaged plants ($P < 0.01$), but on older plants there were no significant differences between affected and unaffected plants in the numbers of buds and bolls present.

Schmitz also records that heavy rain reduces the mite population when the plants are young and liable to be splashed by mud. At Serere a population of 20–30 mites per leaf on cotton three months old was reduced to nil overnight by a rain storm of $1\frac{1}{2}$ inches; unfortunately the fate of any eggs is not known, but there was no reinfestation of this cotton.

Summary.

The damage caused to cotton by the yellow tea-mite, *Hemitarsonemus latus* (Banks), was first seen in Uganda in 1945 and is now known throughout the important cotton-growing areas of the country. Experiments on cotton in the

Belgian Congo showed that sprays and dusts of several insecticides would control or prevent infestations of *H. latus*; earlier published work in Uganda suggested that BHC reduced tea-mite damage and DDT increased it, when both were applied as sprays from wettable powders. However, tea-mite damage was not noticeable on trials in which single rows of cotton were sprayed with DDT emulsion, or on large-scale trials using DDT formulated as a water-miscible liquid. These trials were all directed against the pest insects *Earias* spp. and *Lygus vosseleri* Popp., the standard rate of application being 1 lb. active ingredient per acre applied four times at ten-day intervals.

Results are given of three trials at Serere, Uganda, in 1959, in which certain plots were protected against insect pests (*Earias* spp. and *L. vosseleri*) by DDT applied in a miscible-liquid formulation at the rate of 1 lb. active ingredient per acre *per application*, the numbers and timings of the application differing in the three trials. Tea-mite damage was estimated as the numbers of plants showing any symptoms on sample plants taken at random. In each trial there was less tea-mite damage on the sprayed plots, and the reduction was highly significant in two of the trials. One of the latter was a plant spacing trial; the tea-mite damage did not vary significantly with plant spacing on sprayed plots, but on the unsprayed cotton the amount of damage, measured as the number of plants showing any visible symptoms, rises with wider spacing. This appears to be a contradiction of results obtained in the Congo.

As yet no trials have been done using only acaricides having no effect on insects, to try to distinguish between any reduction in yield that may be due to mites as compared with that due to insects. Results of examinations of cotton plants with and without symptoms of tea-mite attack suggest that although *H. latus* may cause some early loss of fruiting bodies, the plants subsequently recover and form more fruiting bodies; moreover, in unsprayed cotton, plots of widely spaced plants, although showing the highest tea-mite damage, gave the highest yield. *H. latus* is recorded as causing yield reductions of up to 70 per cent. in the Congo, but such effects are not experienced in Uganda.

Acknowledgements.

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References.

- COAKER, T. H. (1956). Entomology.—*Progr. Rep. Exp. Stas Emp. Cott. Gr. Corp.* 1955–56 Namulonge pp. 24–29.
- FJELDDALEN, J. (1951). Røykemidler mot skadedyr i veksthus.—*Meld. Planterv., Oslo* no. 6, 20 pp. (Seen only as abstract in *Rev. appl. Ent.* (A) **41** p. 6.)
- GADD, C. H. (1946). Observations on the yellow tea-mite *Hemitarsonemus latus* (Banks) Ewing.—*Bull. ent. Res.* **37** pp. 157–162.
- McKINLAY, K. S. (1954). The design of insecticide field trials on cotton in Uganda.—*Proc. 6th Symp. Colston Res. Soc.* pp. 53–59.
- MICHELMORE, A. P. G. (1954). C. Section of Entomology. Yellow tea mite, *Tarsonemus latus* Banks (Acarina).—*Rec. Invest. Dep. Agric. Uganda* no. 3 (1950–52) pp. 51–52.
- PEARSON, E. O. (1958). The insect pests of cotton in tropical Africa.—355 pp. London, Emp. Cott. Gr. Corp. & Commonw. Inst. Ent.
- SCHMITZ, G. (1956). L'acarirose du cotonnier.—*Bull. INEAC* **5** pp. 329–339.

- SMITH, F. F., FULTON, R. A. & HALL, S. A. (1950). Toxicity of organic phosphates to the two-spotted spider mite and the foxglove aphid.—*J. econ. Ent.* **43** pp. 627–632.
- THOMAS, D. G. (1956). B. Section of Botany and Pathology. II. Yellow tea mite (*Tarsonemus latus*, Banks) on cotton.—*Rec. Invest. Dep. Agric. Uganda* no. 4 (1952–54) pp. 8–9.
- VRYDAGH, J. M. (1942). Étude de l'acariose du cotonnier, causée par *Hemitarsonemus latus* (Banks) au Congo Belge.—*Publ. Inst. nat. Étude agron. Congo Belge* Sér. sci. no. 28, 25 pp.
- WATSON, T. Y. (1953). Annual report of the Department of Agriculture, Uganda Protectorate, for the year ended 31st December, 1952.—76 pp. Entebbe.

THE EFFECT OF TEMPERATURE ON THE CONSUMPTION OF FAT DURING PUPAL DEVELOPMENT IN *GLOSSINA*.

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Pl

The larva of the tsetse fly is nourished by a maternal secretion rich in lipoid (Hoffmann, 1954) and at the time of deposition it contains extensive reserves of chloroform-soluble substances, which will henceforth be referred to as fat. This fat constitutes the sole source of energy during pupal development (Bursell, 1958) and that which remains at the end of development makes up the greater proportion of the food reserves available to the fly prior to its first blood-meal. It is clear that any factor which affects the amount of fat consumed during development will influence the length of life of the newly emerged fly and hence its chance of obtaining a blood-meal. Temperature could be such a factor and, to estimate the magnitude of the effect, the fat content of newly emerged flies was determined following development at different temperatures.

Material and methods.

Most of the experimental work was done with puparia† of *Glossina morsitans* Westw. bred from females maintained in the laboratory. Puparia were recovered from the breeding tubes and weighed less than 10 hours after larviposition; they were kept in incubators at the stated temperatures until the flies emerged. The normal rhythm of emergence (Bursell, 1959a) appears to be abolished when puparia are kept at constant temperature, the flies emerging indifferently at all hours. The incubators were inspected at regular intervals from early morning till about 2200 hr., so that during this period flies were recovered soon after emergence. They were kept under observation at about 25°C. until they had reached the stage of being capable of flight and were then killed with potassium cyanide. Of the flies that emerged during the night, only those that were not yet capable of flight at the first inspection were included for analysis.

After the flies had been killed, fat content and non-fatty dry weight (referred to as residual dry weight) were estimated by methods described elsewhere (Bursell, 1959a). Regressions of fat contents on residual dry weight were calculated and samples compared at specified levels of this measure of size. As will be shown below, the relation between size and fat content is not rectilinear over the whole range of size, but within the restricted ranges over which regressions were calculated this departure from rectilinearity was not statistically demonstrable, and failure to take account of it is unlikely to affect the conclusions drawn.

In attempting to relate present findings to the biology of tsetse flies under natural conditions it will be assumed that normal shade temperatures give a

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† To avoid continual circumlocution, the word "puparium" will be used to denote the puparial shell and its contents, whether these comprise a third- or fourth-instar larva, a pupa or pharate adult.

fair indication of the conditions experienced by puparia. Very little information is available regarding the microclimate of pupal sites; Nash (1942) showed that pupal-site temperatures in the habitat of *G. morsitans* and *G. tachinoides* Westw. in West Africa were usually somewhat lower than shade temperatures. On the other hand, records (unpublished) made during the hot season in a breeding site of *G. pallidipes* Aust. in Shinyanga, Tanganyika, showed the opposite relation. It seems likely that no single relationship will be generally valid, and in the absence of further information shade temperatures may be regarded as a reasonable first approximation to pupal-site temperatures.

For comparative purposes puparia collected in the field were used; the sources of puparia of the different species have been listed elsewhere (Bursell, 1958).

TABLE I.

The relation between fat content and residual dry weight of newly emerged *Glossina morsitans* subjected to different developmental temperatures, with some data on the fat content of the newly deposited larvae and the weight of puparial shells.

Regression (Y on X)		Temp. °C.	N	\bar{y} mg.	\bar{x} mg.	b	Variances	
							$s^2_{y.x}$	Sx^2
A. Newly emerged flies								
1958	Fat on RDW ..	30.3	18	0.516	3.63	0.3171	0.0148	3.95
	” ” ” ..	27.0	20	0.555	3.58	0.3977	0.0167	5.46
	” ” ” ..	24.9	21	0.655	3.43	0.4709	0.0246	6.46
	” ” ” ..	21.7	16	0.671	3.89	0.4957	0.0161	6.06
	” ” ” ..	19.6	14	0.621	3.86	0.4805	0.0224	4.34
1957	” ” ” ..	30.4	32	0.505	3.87	0.3105	0.0156	8.55
	” ” ” ..	30.3	24	0.516	3.69	0.2692	0.0142	5.27
	” ” ” ..	28.9	20	0.816	4.06	0.4104	0.0276	7.83
	” ” ” ..	25.9	28	0.627	3.59	0.3758	0.0165	6.00
B. Newly deposited larvae								
	F_L on RDW_L ..	—	28	2.820	5.89	0.4378	0.0568	18.78
	RDW_T on OW_P ..	—	75	3.618	22.40	0.1625	0.0376	839.01
C. Puparial shells								
	SW_P on OW_P ..	—	21	1.488	22.91	0.0650	0.0054	132.41

Y = dependent variable and \bar{y} = mean of dependent variable

X = independent variable and \bar{x} = mean of independent variable

N = number of observations

b = coefficient of regression of Y on X

For other abbreviations, see p. 587.

The standard error of b is given by $\sqrt{\frac{s_{y.x}^2}{Sx^2}}$

The standard error of \bar{y} is given by $\sqrt{s_{y.x}^2/N}$

The standard error of \hat{Y} is given by $\sqrt{s_{y.x}^2 \left(\frac{1}{N} + \frac{(X - \bar{x})^2}{Sx^2} \right)}$

Results.

The effect of temperature on the fat consumption of puparia of *G. morsitans*.

A preliminary analysis of results showed that the relation between the deposition weight of puparia and the residual dry weight of the emerging flies

was unaffected by temperature; but there was a slight sex difference in that female puparia of original weight 22.442 mg. produced teneral flies with a residual dry weight of 3.660 mg., while the corresponding value for males was 3.560, the difference being significant at the 5 per cent. level ($t = 1.95$; $n = 67$). This would appear to be the basis of a sex difference previously reported by Jack (1939) and Buxton & Lewis (1934), and since confirmed for several species in this laboratory, namely, that the fat content of newly emerged female flies, expressed as a percentage of the total dry weight, is slightly less than that of males of the same size. The magnitude of the difference is such that it could be accounted for by the above-mentioned difference in residual dry weight; in other words, females do not have less fat than males, but they have more residual dry weight, so that when their fat content is expressed as a percentage of total dry weight, it appears smaller.

In determining the effect of temperature on fat consumption it seemed permissible to ignore this slight sex difference, especially since sex ratios never differed significantly from 1:1 and showed no tendency to vary systematically with temperature; the results for males and females have accordingly been combined.

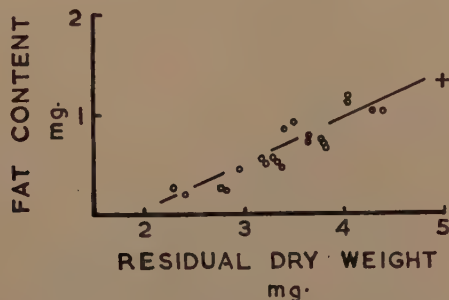


Fig. 1.—The relation between fat content and the residual dry weight of newly emerged teneral adults of *Glossina morsitans* after development at 24.9°C. + = fat content of flies with a residual dry weight of 5.0 mg., as estimated by the method outlined on p. 589.

Fig. 1 shows the relation between the residual dry weight and the weight of fat in newly emerged teneral flies developed at 24.9°C., and illustrates the kind of data on which the present investigation is based. The line is given by the formula of regression, particulars of which for this and other temperatures are set out in Table I(A). Puparia of the 1958 experiments were derived from a single population of females and were assigned to the different incubators in rotation in order to allow for possible changes in the amount of fat laid down during successive pregnancies. No such change could be detected, nor do the results differ appreciably from preliminary experiments done in 1957 under slightly different conditions of maintenance, and it has been thought legitimate to consider the data as homogeneous.

Given the regression coefficients in Table I(A) it is possible to calculate the amount of fat present in flies of a given size at each temperature. The size chosen was 3.60 mg. residual dry weight which is near to the mean for the group as a whole (see column 5) and the values have been plotted in

fig. 2. Some data from Jack (1939), corrected for size in the same way, have been included for comparison, and are in reasonably close agreement. The results show that the fat content of newly emerged flies is highest when development has taken place at about 24°C.

In order to get an estimate of the consumption of fat it was necessary to compare the fat content of newly emerged flies with that of the newly deposited larva. This comparison is complicated by the fact that parts of the larva, those destined to form the puparial shell, the 4th-instar exuviae and the pupal skin, do not enter into the composition of the fly. In order to find the fat content of the part that does, henceforth referred to as the presumptive teneral, it was necessary to estimate first the contribution made by the larval

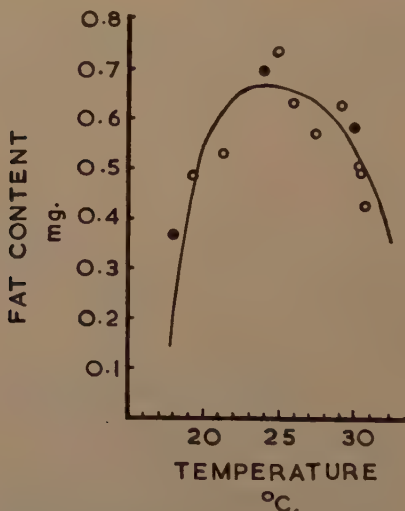


Fig. 2.—The fat content of newly emerged adults of *G. morsitans* with a residual dry weight of 3.60 mg.

● = data from Jack (1939).

The curve has been drawn on the basis of the relation between rate of fat consumption and temperature, see p. 587.

and pupal integuments to the total residual dry weight and the fat content of the larva. The composition of these integuments, recovered after emergence of the flies from puparia of known original weight, was accordingly determined; their fat content, amounting to about 0.01 mg. per puparial shell, could not be estimated accurately with the balance available, and only residual dry weight has been considered; the relation between this and the original weight of puparia is shown in Table I(C).

Table I(B) gives the relation between the original weight of puparia and residual dry weight of the newly emerged flies (combined for male and female). A slight increase in residual dry weight occurs in the course of development (Bursell, 1958), but since it amounts to less than 0.2 mg. it has for present purposes been ignored, and the residual dry weight of the teneral taken as equal to the residual dry weight of the presumptive teneral. Given all these relations, the fat content of the presumptive teneral may be calculated. Thus,

if RDW = residual dry weight, SW = weight of puparial shell and other exuviae, OW = original weight and F = weight of fat, with the subscript T denoting teneral, P puparium, L larva and PT presumptive teneral, then from Table I(B)

$$RDW_{PT} = RDW_T = 0.1625 OW_P - 0.022 \quad \dots \quad (1)$$

$$\text{and from Table I(C) } SW = 0.06504 OW_P - 0.002 \quad \dots \quad (2)$$

Since the fat content of the exuviae is negligible the fat content of the larva will equal that of the presumptive teneral; and the residual dry weight of the larva equals that of the teneral *plus* that of the puparial shell and other exuviae, thus from Table I(B)

$$F_L = 0.4378 RDW_L + 0.240 \quad \dots \quad (3)$$

$$\text{or } F_{PT} = 0.4378 (RDW_T + SW) + 0.240 \quad \dots \quad (4)$$

By substituting for SW in (4)

$$F_{PT} = 0.4378 RDW_T + 0.02848 OW_P + 0.239 \quad \dots \quad (5)$$

and for OW_P in (5)

$$F_{PT} = 0.6131 RDW_T + 0.243 \quad \dots \quad (6)$$

From this formula the fat content of a presumptive teneral with a residual dry weight of 3.60 mg. will be 2.450 mg., and the fat consumption at different temperatures is given by the difference between this amount and the values shown in fig. 2; it varies between about 2.0 mg. at 30°C. and 19°C. and 1.8 mg. at 25°C.

Knowing the relation between temperature and the duration of the pupal period (Jackson, 1949), the rate of fat consumption can now be calculated at the different temperatures. The logarithm of this rate (mg. fat/100 days) has been plotted against temperature in °C. (T) as (i) in fig. 3a; the relation is obviously rectilinear over the range of temperatures under consideration, and it is expressed by the formula

$$\log \text{ rate} = 0.03623T - 0.1463 \quad \dots \quad (7)$$

In view of the close fit obtained in fig. 3 a(i) it is possible with some confidence to work back from this regression to obtain the amount of fat that would be left in teneral flies at temperatures other than those used; the results have been plotted as the smooth curve in fig. 2. The calculations have been extended to cover the whole of the range of viable temperatures, an extension which has involved some slight extrapolation from the log rate/temperature plot in fig. 3. It would have been desirable to have had experimental data at extremes of the range, but such data would have been of very doubtful significance. It has been shown elsewhere (Bursell, 1959a) that a fat content of 4.4 per cent. of the total dry weight represents the lethal limit. Reference to the raw data of the present study shows that this value is closely approximated by smaller flies at temperatures of 19 and 30°C., which represent the extremes of the experimental series. It is clear that outside this range the smaller individuals would be subject to heavy selection on the basis of fat content, and this would result in false estimates both of regression coefficients and of mean fat content.

The mean residual dry weight of newly emerged teneral flies in the field varies between 4.5 and 5.5 mg., depending on the season (see, for instance, Jack, 1939), and flies as small as those represented in the curve of fig. 2 are seldom encountered under natural conditions. Given the regression coefficients shown in Table I it is possible to get some idea of the amount of fat which would be left to flies of normal size; but small errors in the estimates of regression coefficients will give rise to large errors in the estimates of fat content, and, in addition, the variance of estimates increases as the square of the distance from

the mean value of residual dry weight, so that it would be impossible to place much reliance on results obtained in this way.

If the data are to be extended to cover flies of different size, and perhaps species of different size, a consideration of the basic relations between

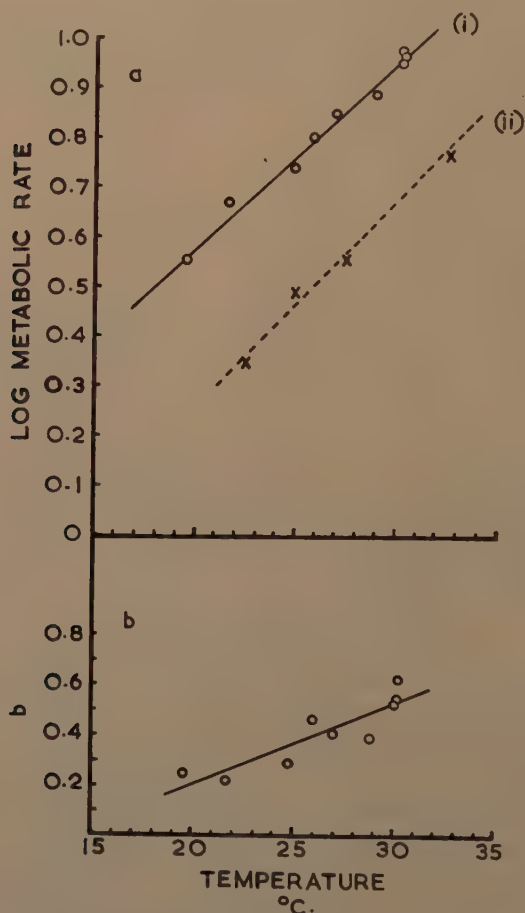


Fig. 3.—The effect of temperature on metabolic rate in *G. morsitans*. a, the relation between the logarithm of the metabolic rate and temperature, for (i) pupal development (mg. fat/100 days), (ii) resting teneral flies (mg. fat/10 days); b, the coefficient of regression of log metabolic rate on log residual dry weight as a function of temperature.

respiratory rate and size at different temperatures, of which fat content at emergence is the final effect, would seem more promising.

The relation between size and fat consumption at a given temperature may be obtained from the data given in Table I, over the narrow range of size

represented in laboratory-bred puparia. It is clearly given by the difference between the regression coefficient of the teneral flies and that of the presumptive tenerals. Since neither departs significantly from rectilinearity over the range in question, the regression of fat consumption on size will also be linear and so will the regression of rate of fat consumption, that is to say, respiratory rate, on size. It would not, however, be safe to assume that this apparently linear relation would hold over a bigger range of size. The relation between size and oxygen consumption has been studied in many different animals and it is usually found that, when a wide range of size is available, a double logarithmic plot is necessary to give a rectilinear relation (see for example Ellenby & Evans, 1956; Balke, 1957; Kienle, 1957; Berg, Lumbye & Ockelmann, 1958; Edwards, 1958); this has been so widely substantiated that it seems permissible to regard it as a general characteristic of respiration. It is not at variance with such data as are available for *Glossina* and the calculations that follow will be made on the basic assumption that the log rate of fat consumption is linearly related to the logarithm of the residual dry weight over the whole of the size range.

On the basis of the data given in Table I, the coefficients of regression of log rate on log size has been calculated. The values seem to be markedly affected by temperature, a phenomenon which is reflected in the inverse relationship between temperature and the regression coefficients of fat content shown in Table I, column 6. It seems, in other words, that the higher the temperature the greater is the increase in respiratory rate for a given increase in size. The relationship between b , the regression coefficient of log fat consumption on log size, and temperature (T) is shown in fig. 3 b; it is given by the formula

$$b = 0.03247T - 0.4470 \quad \dots \dots \dots (8)$$

and the regression is highly significant, the standard error of the coefficient being 0.00608 ($t = 5.3$).

If we accept the relations shown in (7) and (8) it is possible to calculate what would be the fat content of flies with a residual dry weight of 5.0 mg., equal to that of tenerals emerging in the field. Thus formula (8) will give the increase in log rate per unit increase in log residual dry weight at a given temperature, and multiplying by 0.1427, which is the difference between log 3.6 and log 5.0, we get the log rate increment. This is added to the log rate at 3.6 mg., as given by formula (7) for the temperature in question, to give the log rate at 5.0, and, knowing the original fat content of the presumptive teneral, the fat content of the emerging fly.

At 24.9°C. the value estimated in this way is 1.30 and reference to fig. 1 indicates that, for the species concerned, this represents a good prediction of the fat content of individuals just outside the size range covered; it is reasonable to hope that the considerations on which this estimate is based will provide a valid basis for interspecific as well as intraspecific correction for size.

Comparative aspects of pupal metabolism.

The fat content of newly emerged tenerals of different species is shown in Table II A. Puparia of *G. swynnertoni* Aust. were collected at Shinyanga, where this work was carried out; the other species were sent by post from the collecting areas listed in Bursell (1958) and maintained on arrival at a temperature of about 25°C. The collections were made between April and August; at that time of the year mean shade temperatures would be unlikely to differ from 25°C. by amounts sufficient to cause a significant decrease in fat content, and in what follows it will be assumed that the puparia were maintained throughout at that temperature.

It is clear in the first place that the value for *G. morsitans* is much higher than one would expect on the basis of the results discussed earlier in this paper,

which showed the fat content of laboratory-bred teneralis of size 5.30 mg. maintained at 25°C. to be about 1.5 mg. (see fig. 1); the comparable figure from Table II for teneralis bred in the field is 2.20 mg. The reason for such a discrepancy could be either that more fat is laid down during pregnancy under natural conditions, or else that the relation between fat and size is not rectilinear over the whole range of size. Inspection of the data suggests that the latter is the correct alternative; for, confining our attention to the samples that were large enough for reliable estimation of regression coefficients, it is clear that the latter tend to be related to size, with values for *G. pallidipes* of about 0.9, for *G. morsitans*, *G. swynnertoni* and *G. palpalis* (R.-D.) of about 0.6–0.7 and for laboratory-bred *G. morsitans* (see Table I) of 0.4–0.5. A similar trend shows in

TABLE II.

The relation between fat content and residual dry weight in newly emerged flies and in larvae of some species of tsetse fly.

Species	N	\bar{y} mg.	\bar{x} mg.	b	Variances	
					$s^2_{y.x}$	Sx^2
A. Newly emerged flies						
<i>G. swynnertoni</i> ..	48	1.77	4.93	0.779	0.060	7.24
<i>G. palpalis</i> ..	49	1.83	4.90	0.557	0.092	8.63
<i>G. morsitans</i> ..	25	2.20	5.30	0.726	0.070	2.88
<i>G. pallidipes</i> ..	21	3.42	6.42	0.902	0.121	4.98
<i>G. austeni</i> ..	17	1.66	3.39	0.742	0.056	4.97
<i>G. longipennis</i> ..	7	4.04	13.82	0.171	0.092	4.19
<i>G. fuscipleuris</i> ..	4	3.96	11.06	0.321	0.095	4.51
B. Newly deposited larvae						
<i>G. swynnertoni</i> ..	17	1.91	4.61	0.496	0.021	7.67
<i>G. morsitans</i> ..	28	2.82	5.89	0.438	0.057	18.78
<i>G. pallidipes</i> ..	14	3.65	7.62	0.614	0.120	38.03

Symbols as for Table I.

the data for laboratory-bred larvae (Table II(B)). Thus it appears that the relation between fat and residual dry weight should be represented by a curve convex to the abscissa, and adopting values for the slope of 0.5 at size 3.5, 0.7 at size 5.0 and 0.9 at size 6.5 the data for *G. swynnertoni*, *G. palpalis*, *G. morsitans* and *G. pallidipes* fit well on a single curve as shown in fig. 4 (curve 1).

This relation between residual dry weight and fat in newly emerged tsetse flies illustrates very clearly a phenomenon noted many years ago by Mellanby (1936), namely, that smaller flies have lower proportions of fat. From the graph it can be calculated, for instance, that flies emerging with a residual dry weight of 4.0 mg. have a fat content, expressed as a percentage of total dry weight, of 20 per cent., while those whose residual dry weight is 7.0 mg. have a fat content of 37 per cent. Mellanby concluded that the amount of fat consumed by large and small puparia must have been about the same; but this, of course, does not follow, nor is it in fact the case (see above). It is, however, clear that, since oxygen, and hence fat, is consumed in proportion to residual dry weight (Bursell, 1959a), smaller species within the group under consideration, and smaller individuals within a species, will be at a disadvantage in respect of fat reserves.

Accepting fig. 4 (curve 1) as a reasonable estimate of the relation between size and fat in teneralis developed at 25°C. it is possible, using the formulae described above, to calculate what would have been the fat content of the presumptive teneralis. This curve is shown in fig. 4 (curve 2), and the very close agreement with the experimental values for *G. swynnertoni* and *G. pallidipes* may be taken as evidence for the validity of the assumptions made. Agreement with the value for *G. morsitans* has no significance since this value was used in the computations on which the curve was based. Using

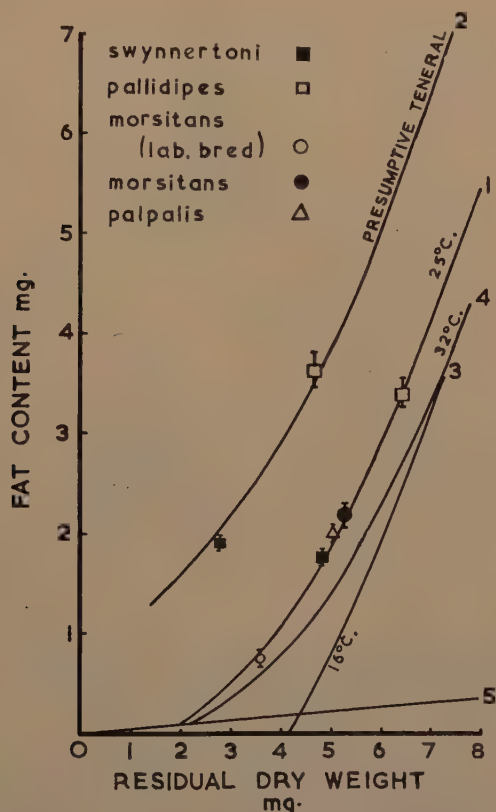


Fig. 4.—The fat content of presumptive teneralis of different species of *Glossina* (2), and of newly emerged flies developed at 25°C. (1), 16°C. (3) and 32°C. (4); the critical fat content (4.4%) is represented as curve (5).

the curve thus obtained for presumptive teneralis it is possible to reverse the procedure and calculate the teneral fat content at other temperatures. The values chosen were 16°C., which is close to the minimum mean temperature likely to be encountered under natural conditions (Du Toit, 1954) and 32°C., which is close to the maximum (Jack, 1941). The values obtained have been plotted as curves 3 and 4 in fig. 4. Since the difference between flies developing at 25°C. and at the optimum is negligible (see fig. 2) differences between curves 1, 3 and 4 may be taken to represent the difference between optimal conditions and extremes of heat and cold. This is seen to amount to between 0.5 and 1.0

mg., which is a very substantial proportion of the total reserves of the teneral fly. The curves also show that for smaller species a shift towards the cold extreme is much more deleterious than a shift towards the hot extreme, while for larger species either change produces about the same effect.

The point at which curves cross the 4.4 per cent. line (curve 5 in fig. 4) represents the size at which fat reserves are exhausted before development is complete, and the flies fail to emerge. Such points of intersection have been calculated for a number of temperatures and are plotted in fig. 5 (curve a). For the group of species under consideration, the maximum size is about 8.0 mg.

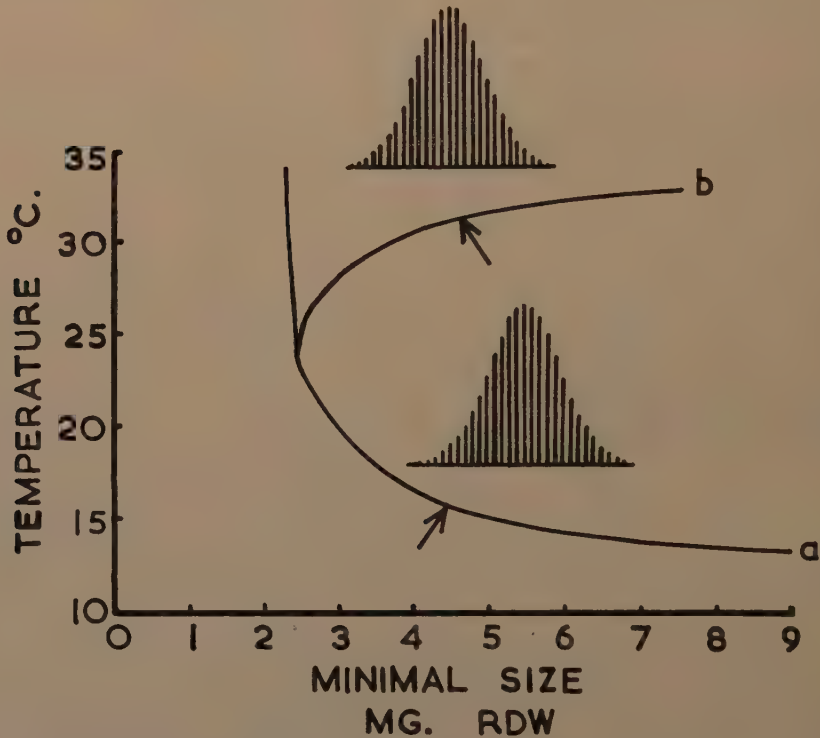


Fig. 5.—The size at which fat reserves are exhausted before development has been completed (a), or before a blood-meal can be obtained (b). The frequency distributions of size for summer and winter populations of *G. morsitans* have been included in the figure, and the maximum mean summer and minimum winter temperatures likely to be encountered within the distribution limits of this species have been marked by arrows. For further explanation see text.

residual dry weight, and the curve shows that the critical temperature for such flies is 14°C. This estimate of the minimal temperature which will permit development to reach completion is considerably lower than values (18–20°C.) reported to represent the threshold for development (see Buxton, 1955). But it must be remembered that previous estimates have been based on laboratory-bred puparia of the smaller species of tsetse fly whose mean size seldom exceeds 4.0 mg. residual dry weight (Jack, 1939; Mellanby, 1936; Potts, 1933); reference to fig. 5 shows that at this size the lower threshold would be expected to be about 17°C.

At temperatures near the upper extreme of the viable range the critical size is nearly constant at about 2.3 mg., a size which is seldom if ever encountered under natural conditions. But it must be borne in mind that though fat reserves may be sufficient to enable emergence from the puparium, the flies have also to rely on such reserves until they can obtain their first blood-meal. Since emergence shows a marked diurnal periodicity with peak values at about 1600–1700 hr. East African Standard Time, leaving less than 4 hr. of daylight (see Bursell, 1959a) and since the flightless period lasts about 1.5 hr. even at high temperatures (Bursell, unpublished) it is clear that unless fat reserves are sufficient to last overnight the chances of flies getting a blood-meal will be extremely small. The relation between temperature and resting fat consumption, determined according to methods described elsewhere (Bursell, 1959a), has been included, as (ii), in fig. 3a, and from the data it is possible to estimate the critical size of flies, such as will allow survival for 15 hr. after emergence, that is, until dawn the following day. At low temperatures the resting fat consumption is very small and the curve does not differ appreciably from that shown as curve (a) in fig. 5; but above 24°C. the difference becomes appreciable and the curve rises sharply at still higher temperatures (fig. 5, curve (b)).

The mean size of *G. morsitans* during the hot and cold seasons in Southern Rhodesia (data from Jack, 1939) have been included in fig. 5, together with the normal frequency distributions. Meteorological records are available from the same region (Jack, 1941) which, in conjunction with data published in the earlier paper, show that the mean winter temperature may be below 16°C. for about three months of the year (the pupal period at 16°C. is just over three months), while the mean temperature during the hottest months may be close to 32°C.; these values have also been marked by arrows in fig. 5. It is clear that during the winter some of the smallest puparia will have insufficient fat to complete their development, while during the hot season all but the largest will have exhausted their reserves before they have a chance to obtain a blood-meal. In view of these relations there can be little doubt that the exhaustion of pupal fat reserves may be an important limiting factor for *G. morsitans* under natural conditions.

The mean size of *G. swynnertoni* is about 0.5 mg. less than that of *G. morsitans* and its tolerance range would be correspondingly smaller. Its distribution is such that it would be unlikely to be subjected to mean temperatures near its lower minimum, except perhaps in local situations at high altitude, but during the hot season mean temperatures often exceed 28°C. in its natural habitat, and a heavy selection for size could be expected. In this connection it is of interest that Jackson (1948) has reported a slight but significant selection for size during the early part of the hot season in Shinyanga, attributing the phenomenon to elimination of small tenerals.

The mean size of *G. pallidipes* in the cold season is over 6.0 mg., which makes its lower minimum just over 14°C. (see fig. 5); within the limits of its distribution this value would never be maintained long enough to cause critical depletion of fat reserves (pupal period would be 256 days). Even under hot-season conditions the margin of safety is considerable and only a low intensity of selection for size could be expected, if any.

The close relation between size and the range of temperature over which development can proceed to completion, represented by the vertical distance between curves (a) and (b) in fig. 5, is perhaps of relevance to the distribution of the species under consideration. It may not be without significance, for example, that where *G. pallidipes* overlaps with *G. swynnertoni*, for example, near the Mara River, Kenya (Dr. J. P. Glasgow, personal communication) or with *G. palpalis* (Lewis, 1939), the larger species appears to have the higher altitude limit. And again, *G. pallidipes* is the species which has extended furthest

into the temperate zones south of the Equator, reaching 28°S. in Zululand; the corresponding limit for *G. morsitans* is 21°S. and for *G. palpalis* 11°S., while *G. swynnertoni* does not extend south of the 5° latitude. In many instances the distribution limits will, of course, be set by factors other than climate—vegetation for instance, or the presence of host animals in sufficient density, or chance. But the above relations are in accord with the possibility that the exhaustion of pupal fat reserves may have played a part in limiting the distribution of *Glossina*.

Table II includes some data for *G. austeni* Newst., *G. longipennis* Corti and *G. fuscipleuris* Aust. The fat content of *G. austeni* is clearly far greater than one would have expected for a fly of its size (cf. curve 1 of fig. 4). Residual dry weight ranges from 2.3 to 4.3 mg. and reference to fig. 5 shows that, had *G. austeni* conformed to the relations obtaining for the species already discussed, the smaller individuals would have been unable to complete their development even under optimal conditions (24°C.). It seems that the reduction in size exemplified by *G. austeni*, and also by *G. tachinoides* (Buxton & Lewis, 1934), has of necessity been accompanied by a change in the proportion of fat to residual dry weight laid down during pregnancy. A similar difference seems to characterise other members of the *morsitans* and *palpalis* groups as compared with the larger species of the *fusca* group; the latter have far less fat than would have been expected from the relation shown in fig. 4, but the data in respect of these large species are insufficient to warrant further discussion.

Delayed emergence.

Recent field studies in South Africa (Du Toit, 1954) have led to the suggestion that during the winter months emergence of *G. pallidipes* may be prevented by maximum temperatures failing to exceed the threshold for emergence (about 16°C., see Jackson, 1946), and that mass hatching may occur in spring with the onset of warmer weather. Investigation of the fat consumption of pharate adults whose emergence had been prevented by maintaining them at temperatures of about 15°C. showed that depletion of fat reserves occurred fairly rapidly in spite of the low temperature. This is a reflection of the high metabolic rates which characterise the end of pupal development in *Glossina* (unpublished observation) as in many other insects (cf. Roeder, 1953). Puparia of *G. morsitans* maintained for two weeks under these conditions lost nearly 0.5 mg. fat, and it is clear from fig. 4 that under natural conditions, when pupae would have been subjected to low mean temperatures throughout development, fat content would reach the critical level in about three weeks. The phenomenon of delayed emergence is thus unlikely to be of much importance in the smaller species. These results incidentally show that the practice of chilling pupae in order to ensure mass emergence over a short period of time (Jackson, 1946, 1948) is a questionable one.

Theoretically the duration of delay might be extended in *G. pallidipes*, whose fat reserves are greater than those of *G. morsitans*, and an attempt was made to get some idea of the time factor involved in the Zululand results. The concept of delayed emergence was based on the observation that the percentage of "mature" pupae collected increased markedly during the winter months. The category defined by the South African workers as "mature" corresponds to Stage III, 4b of Bursell (1959b) and its duration is 7.4 per cent. of the pupal period, in good agreement with the mean value of 7.8 per cent. obtained for *G. pallidipes* during the months for which delayed emergence could not be expected (July to April). During the winter months of May and June the percentage rose to 14.4, and a simple calculation will show that with a mean pupal period of 90 days (see fig. 1 in Du Toit, 1954) a delay of 6 days would account for the observed increase. It would appear that the phenomenon of delayed emergence has played little part in the transient increase in trap catches

which occurs at the onset of warm weather in Zululand; such an increase might indeed be adequately accounted for by a progressive increase in temperature with consequent acceleration of pupal development.

Thermal thresholds of development.

The range of temperatures over which development of the tsetse fly may proceed to completion has not yet been unequivocally settled. At the upper extreme, Potts (1933) found that mortality was doubled by exposure of puparia to 30°C., but no such effect is apparent in the results published by Jack (1939) who worked on the same species of tsetse fly, nor were the mortalities recorded in the course of the present work related to temperature. The mortality of *G. palpalis* is also unaffected by temperatures up to 30°C. (Mellanby, 1936), whereas with *G. tachinoides* a deleterious effect has been reported (Buxton & Lewis, 1934), although in this case only the smaller individuals appeared to be affected.

At the lower end of the temperature range, little work has been done, but 18°C. has been suggested as a likely lower threshold (Buxton, 1955) despite evidence of development at lower temperatures relating to *G. pallidipes* in Zululand (Du Toit, 1954).

TABLE III.

The percentage mortality induced by exposure of field-collected puparia to low temperatures.

Temp. °C.	Duration of exposure (days)				
	1	2	3	4	5
+6	8	6	9	13	5
+2	8	12	17	18	32
-1	3	17	23	29	42

The values represent the difference between the mortality at a given level of exposure and the control mortality for the batch under consideration. Control mortalities were estimated with samples of 500 puparia, experimental mortalities with samples of 200 for each treatment.

In view of present findings there can be little doubt that these discrepancies arise in large part from a failure to distinguish between the effect of temperature on the basic mechanism of development and its effect on metabolic rate vis à vis available fat reserves. Thus the correlation between size and mortality noted by Buxton & Lewis (1934) for *G. tachinoides* suggests that exhaustion of food reserves may have played a predominant part, and the discrepancy between the results of Jack (1939) and Potts (1933) could also be due to a difference in mean size between puparia bred at the different laboratories, and hence in their fat reserves. Similarly, the fact that results with smaller species like *G. palpalis* and *G. morsitans* are contradicted by results with *G. pallidipes* may be a reflection of the much greater fat reserves possessed by the larger species. In general it would seem that results obtained with laboratory-bred puparia should be accepted with caution in view of the tendency of such puparia to be much smaller than those bred under natural conditions. Furthermore, unless it can be shown that development has stopped for reasons other than the exhaustion of food reserves, results cannot be considered to fix a general threshold

for development, but will have relevance only to the particular sample under consideration.

The problem of thermal thresholds is evidently not readily amenable to experimental investigation. It is of interest to note, however, that the relation between the logarithm of metabolic rate and temperature is such that the metabolic rate could be expected to be zero at a temperature of 4°C. (see formula (7)). Some experiments were carried out to determine whether exposure to temperatures in this region would have a demonstrable effect on mortality. Batches of puparia collected in the field were exposed to three different low temperatures for varying lengths of time and then returned to normal laboratory conditions (about 25°C.). The percentage mortality is shown in Table III and it is apparent that exposure to 6°C. has caused a slight increase in mortality but that the duration of exposure has been without effect. At 2°C., on the other hand, there is a progressive increase in mortality as the time of exposure is extended from one to five days, and a similar but much more pronounced effect occurs at -1°C. The threshold for this progressive increase in mortality evidently lies between 6 and 2°C. and it is tempting to equate it with the temperature of 4°C. at which the metabolic rate is reduced to zero. In other words, the real threshold of development may be 4°C., but development could never proceed to completion at this temperature because fat reserves, even in the largest species, would be totally inadequate.

Summary.

The size-specific fat content of tsetse flies recently emerged from their puparia was determined and by comparison with the size-specific fat content of newly deposited larvae an estimate was obtained of the consumption of fat during pupal development. Experiments with *Glossina morsitans* Westw. were carried out at a number of different temperatures and it was found that the amount of fat consumed was least at temperatures between 22 and 24°C.

Knowing the duration of the pupal period at different temperatures, the rate of fat consumption could be calculated and the logarithm of this rate was found to be linearly related to temperature. The occurrence of an optimum temperature in respect of fat consumption thus reflects the fact that at high temperatures the rate of fat consumption is greatly increased without a corresponding reduction in the duration of the pupal period, whereas at low temperatures the pupal period is very greatly lengthened without a corresponding decrease in the rate of fat consumption.

It was found that smaller individuals emerge with relatively less fat than larger ones, and the evidence suggests that this is because the amount of fat laid down at the beginning of pupal development is relatively small in small individuals.

The data obtained with *G. morsitans* were extended to cover a number of other species on the assumption that the logarithm of metabolic rate is linearly related to the logarithm of size. The relation between size and fat content in *G. swynnertoni* Aust., *G. palpalis* (R.-D.) and *G. pallidipes* Aust. conforms with that established for *G. morsitans*, the smaller species having relatively small fat reserves. *G. austeni* Newst., on the other hand, has far more fat than would be expected on the basis of this relation, *G. longipennis* Corti and *G. fuscipleuris* Aust. less.

An estimate was made of the size which a tsetse fly must be if it is to complete its development and live to obtain its first blood-meal at different temperatures. Comparison of these estimates with the size distribution of *G. morsitans* and *G. swynnertoni* in cold and hot seasons suggest that exhaustion of pupal fat reserves may play a part in limiting the distribution of these species under extreme climatic conditions.

The logarithm of metabolic rate extrapolates to zero at about 4°C. and at temperatures lower than this the mortality of pupae increases greatly with duration of exposure. It is suggested that 4°C. may represent the lower threshold for the process of development, but that development could never proceed to completion at this temperature because fat reserves would be inadequate.

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References.

- BALKE, E. (1957). Der O_2 -Konsum und die Tracheen-Innenfläche bei durch Tracheenkiemen atmenden Insektenlarven in Abhängigkeit von der Körpergrösse.—*Z. vergl. Physiol.* **40** pp. 413–439.
- BERG, K., LUMBYE, J. & OCKELMANN, K. W. (1958). Seasonal and experimental variations of the oxygen consumption of the limpet *Ancylus fluviatilis* (O. F. Müller).—*J. exp. Biol.* **35** pp. 43–73.
- BURSELL, E. (1958). The water balance of tsetse pupae.—*Phil. Trans. (B)* **241** pp. 179–210.
- BURSELL, E. (1959a). The water balance of tsetse flies.—*Trans. R. ent. Soc. Lond.* **111** pp. 205–235.
- BURSELL, E. (1959b). Determination of the age of tsetse puparia by dissection.—*Proc. R. ent. Soc. Lond. (A)* **34** pp. 23–24.
- BUXTON, P. A. (1955). The natural history of tsetse flies.—*Mem. Lond. Sch. Hyg. trop. Med.* no. 10, 816 pp. London, Lewis.
- BUXTON, P. A. & LEWIS, D. J. (1934). Climate and tsetse flies: laboratory studies upon *Glossina submorsitans* and *tachinoides*.—*Phil. Trans. (B)* **224** pp. 175–240.
- DU TOIT, R. (1954). Trypanosomiasis in Zululand and the control of tsetse flies by chemical means.—*Onderstepoort J. vet. Res.* **26** pp. 317–387.
- EDWARDS, R. W. (1958). The relation of oxygen consumption to body size and to temperature in the larvae of *Chironomus riparius* Meigen.—*J. exp. Biol.* **35** pp. 383–395.
- ELLENBY, C. & EVANS, D. A. (1956). On the relative importance of body weight and surface area measurements for the prediction of the level of oxygen consumption of *Ligia oceanica* L. and prepupae of *Drosophila melanogaster* Meig.—*J. exp. Biol.* **33** pp. 134–141.
- HOFFMAN, R. (1954). Zur Fortpflanzungsbiologie und zur intrauterinen Entwicklung von *Glossina palpalis*.—*Acta trop.* **11** pp. 1–57.
- JACK, R. W. (1939). Studies in the physiology and behaviour of *Glossina morsitans*, Westw.—*Mem. Dep. Agric. S. Rhod.* no. 1, 203 pp.
- JACK, R. W. (1941). Further studies in the physiology and behaviour of *Glossina morsitans*, Westw.—*Mem. Dep. Agric. S. Rhod.* no. 3, 54 pp.
- JACKSON, C. H. N. (1946). An artificially isolated generation of tsetse flies (Diptera).—*Bull. ent. Res.* **37** pp. 291–299.

- JACKSON, C. H. N. (1948). Some further isolated generations of tsetse flies.—*Bull. ent. Res.* **39** pp. 441–451.
- JACKSON, C. H. N. (1949). The biology of tsetse flies.—*Biol. Rev.* **24** pp. 174–199.
- KIENLE, M. L. (1957). Über Beziehungen zwischen Körpergrösse, Lungengrösse und Energiekonsum bei Pulmonaten, insbesondere *Helix pomatia* L. und *Zebrina detrita* Müll.—*Z. vergl. Physiol.* **40** pp. 440–450.
- LEWIS, E. A. (1939). Observations on *Glossina fuscipleuris* and other tsetses in the Oyani valley, Kenya Colony.—*Bull. ent. Res.* **30** pp. 345–358.
- MELLANBY, K. (1936). Experimental work with the tsetse-fly, *Glossina palpalis*, in Uganda.—*Bull. ent. Res.* **27** pp. 611–632.
- NASH, T. A. M. (1942). A study of the causes leading to the seasonal evacuation of a tsetse breeding-ground.—*Bull. ent. Res.* **32** pp. 327–339.
- POTTS, W. H. (1933). Observations on *Glossina morsitans*, Westw., in East Africa.—*Bull. ent. Res.* **24** pp. 293–300.
- ROEDER, K. D. *Ed.* (1953). Insect physiology.—1100 pp. New York, Wiley; London, Chapman & Hall.

THE INFESTIBILITY OF STORED PADDY BY *SITOPHILUS*
SASAKII (TAK.) AND *RHYZOPERTHA DOMINICA* (F.).

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Many statements are to be found in the literature in support of the widely held view that, unlike milled rice and many other grains and pulses, paddy (unhulled, unhusked or rough rice) may be stored for considerable periods without becoming seriously infested by insect pests. Comparing milled rice and paddy, Copeland (1924) states that the latter is "much less subject to (insect) attack" and T. A. Oxley (Rice storage in hot climates.—Paper presented at FAO meeting on rice, 1952) describes paddy as being "almost immune against insect attack". Cheo & Chang (1943) recommend that "where possible, rice should be stored in the husk" since "rice in the husk . . . is rarely infested". Such statements, however, refer almost entirely to paddy produced and stored in India and the East, where, although certain insects such as *Rhyzopertha dominica* (F.) may be described as "major pests of stored paddy" (Ghose, Ghatge & Subrahmanyan, 1956) it does apparently keep relatively free from insect attack. This is not true of paddy stored in the rice-producing regions of the Americas. D. W. Hall (Stored products problems in British Guiana.—Unpublished report, Colon. Off., 1954) states that, contrary to the situation in South-east Asia, India, etc., paddy is obviously heavily infested in store in all the British Guiana mills. Little information exists on the losses caused by insects in stored paddy in the United States, but N. E. Jodon (personal communication, 1959) is of the opinion that "due to storage in bins, a practice which was introduced along with combine harvesting, the infestation in stored (rough) rice is much less and the control much easier than it was when storage was in burlap bags in the warehouse." In British Guiana, paddy storage is entirely in bags, and losses are thought to be high. L. D. Cleare (Rice storage investigations 1955–57.—Dep. Agric. Brit. Guiana, unpublished, 1957) has emphasised the difficulty of estimating losses in stored paddy but has suggested that 4 per cent. of the grain may be destroyed in 12 weeks.

The insects generally considered to be the most important pests of stored paddy are the lesser grain borer, *R. dominica*, the rice weevils, *Sitophilus* spp. and the Angoumois grain moth, *Sitotroga cerealella* (Ol.), but opinions vary as to which of these is the most important. *S. cerealella* is often placed at the head of lists of the major pests of stored paddy in the U.S.A. and according to Douglas (1941) this moth ranks first in importance as an insect injurious to stored rough rice. Although able to infest rice in the field, this moth is essentially a pest of bulk-stored paddy. Its damage is confined mainly to the surface of the bulk and it is of less importance in bagged grain. In British Guiana and Trinidad, losses caused by it appear to be small in comparison with those due to the lesser grain borer and weevils and it is not considered further in this paper.

The literature is also contradictory in regard to the status of *Sitophilus* and *R. dominica* as paddy pests. The older publications such as Douglas (1925) class *Sitophilus* as a primary pest, claiming that "the larvae have strong jaws and easily make their way through the husk or shell of most vegetable products". Balzer (1942), however, states that *Sitophilus* attacks only grains of which the hulls have been broken or have failed to close properly after blooming. In a later paper (Rouse, Rolston & Lincoln, 1958), *Sitophilus* is included with *Rhyzopertha*

among the species that attack sound, whole grain and are capable of doing considerable damage. Cleare (*op. cit.*) states that *Sitophilus* will bore into perfectly sound grains of paddy provided the moisture content is sufficiently high (about 15 per cent.). Corbett & Pagden (1941) were the first to suggest that even *R. dominica* might not be able to attack paddy grains in which the husk is perfectly sound. Their results, from a series of small-scale experiments in which seven species of storage insects were tested on whole and broken paddy and various rice fractions, indicated that perfectly sound paddy was not damaged by any of the insects under observation, but once the husk was injured mechanically by puncture with a needle, *Sitophilus*, *Rhyzopertha* and *Lophocateres* all fed and bred in it. *Lophocateres pusillus* (Klug) commonly infests paddy in British Guiana and Trinidad, but only occurs in any numbers when the grain has been subject to considerable damage by other pests. It can oviposit through narrow cracks in the husk but, when it infests paddy as a primary pest, damage is usually limited to scarification of the pericarp and the periphery of the endosperm or to destruction of the germ. Apart from the work of Chittenden (1916) and H. J. Viljoen (A preliminary investigation into the life history and habits of the Siamese grain beetle (*Lophocateres pusillus* Klug).—Unpublished D.T.A. report, Imp. Coll. trop. Agric., Trinidad, 1957) there is little information on the biology or the status of this beetle. R. T. Cotton (personal communication, 1956) states that it is not sufficiently common in the southern United States to be of economic importance. It is considered to be of less importance than *Sitotroga cerealella* as a pest of paddy in the West Indies, and investigations with this beetle were not therefore undertaken.

It is believed that most of the weevils infesting stored paddy in Trinidad and British Guiana are *Sitophilus sasakii* (Tak.) (formerly referred to as the small strain of *S. oryzae* (L.)), but the characters on which determinations were made, namely size, colour of the abdominal tergites and shape of the spermatheca (Richards, 1944) are not wholly reliable.* Specimens from stock cultures used in the studies here described were, however, submitted to Professor E. H. Floyd of Baton Rouge, U.S.A., and all were found by him to be *S. sasakii*. Some of the weevils used in the experiments were preserved and sent to the Pest Infestation Laboratory, Slough, England, and were there identified likewise as *S. sasakii*. This name is therefore applied to all of the material of *Sitophilus* used in this work. It is possible that *S. sasakii* rather than *S. oryzae* is the principal weevil of stored paddy in the southern U.S.A. Professor E. H. Floyd (personal communication, 1958) states: "very likely when we find the rice weevil in rough rice here it will be the small one".

The present account is of investigations into the infestibility, in relation to *Rhyzopertha dominica* and *S. sasakii*, of varieties of paddy grown in the West Indies and British Guiana. These investigations were undertaken in three stages: (1) an examination of infested samples of paddy in order to determine the principal types of paddy grain (*e.g.*, sound, split, 'green') infested by these two pests, (2) an assessment of the relative infestibility of these classes of grain by exposing them individually or in small samples to infestation under controlled conditions, (3) an attempt to correlate the degree of infestibility of given grain samples to the method of harvest.

Materials and experimental methods.

The parent insect material of both *S. sasakii* and *R. dominica* was obtained from stored seed paddy in Trinidad. Stock cultures of *S. sasakii* were maintained

* The description by Floyd & Newsom (1959) of characters for the separation of *S. oryzae* (L.) from *S. sasakii* (Tak.) was not published until after the completion of the present work.

at 25°C. and 75 per cent. R.H. on high-quality, parboiled, milled rice of even grain size and those of *R. dominica* on bruised Canadian durum wheat at 25°C. and 75 per cent. R.H. and at 29.4°C. and 75 per cent. R.H. The experiments were conducted at three relative humidities, 75, 84.3 and 92.5 per cent., controlled by saturated solutions of sodium chloride, potassium chloride and potassium nitrate, respectively (Stokes & Robinson, 1949). These humidities were maintained in small incubators or in desiccators in larger incubators. A continuous stream of conditioned air was passed through these containers which also held as large a volume as possible of the saturated solution.

All grain used was heat sterilised at a temperature not exceeding 80°C. and was conditioned to equilibrium with a given humidity by exposure in desiccators to a stream of conditioned air. Provided that the layers of the conditioning grain are shallow, equilibration of paddy by adsorption is rapid (Breese, 1955). The separation of infested from good grains in paddy samples was greatly facilitated by the use of a simple flotation technique. The method of Apt (1952) was largely followed, but a saturated solution of magnesium sulphate was substituted for a 2 per cent. (w/v) ferric nitrate solution. This solution has a density of 1.304, *i.e.*, just below that of good grain of the varieties of paddy commonly grown in the West Indies, at between 13 and 14 per cent. moisture content. Many other grains, (*e.g.*, 'green', pecky, fungus-attacked) in addition to those infested, float, but the amount of grain requiring immediate examination is greatly reduced.

For the microscopic examination of paddy samples, a piece of apparatus was constructed by means of which a stream of grains could be passed over the microscope stage. This consisted essentially of an endless belt on to which a single-grain stream of paddy could be directed from a small hopper. The writer is indebted to Dr. H. E. Gray of Ottawa for the original idea of this apparatus. For experiments in which individual grains of paddy were exposed to single females of *R. dominica*, brick slabs similar to those employed by Birch (1945*b*) were used. Each slab measured approximately $3\frac{1}{4}" \times 1\frac{1}{4}" \times \frac{1}{4}"$ and had six depressions or 'cells' into each of which a paddy grain would fit fairly snugly. The face of each slab was ground flat and the cells were so spaced that they could all be covered by a $3" \times 1"$ microscope slide held in place by two rubber bands. The slabs were made from a local brick clay, and the cells formed by pressing in paddy grains glued to the end of short pieces of wood (toothpicks). Allowance had to be made for the shrinkage of the cells during the air-drying of the clay. Paddy grains do not swell sufficiently when wet to allow them to be left in the cells during the drying period—the method used by Birch with wheat grains. After air-drying, the slabs were fired in a muffle furnace, so regulated that a temperature of between 900 and 1000°C. was reached in six hours. The furnace was then switched off and a cooling period of between six and eight hours allowed. These slabs proved very porous and sufficiently hard to prevent adults of *R. dominica* boring into them. Before use, they were conditioned by long exposure to the temperatures and humidities of the experiments. The varieties used in most experiments, *viz.*, Sughandi, D110 and D52/37, were harvested from rogued pure-line seed-production plots and the samples were as pure as could be obtained. When a varietal name or symbol is given elsewhere it merely indicates that the sample was composed in the main of that variety.

Identification of infestation.

The damage caused to the grain by the four 'primary' pests of paddy, *viz.*, *Rhyzopertha dominica*, *Sitophilus sasakii*, *Sitotroga cerealella* and *Lophocateres pusillus* is fairly distinct, so that grains that have been attacked by them may be recognised even in the absence of a living insect within the kernel.

Types of damage.

(a) *Rhyzopertha dominica*.—A normal-sized rice kernel is not, as is often stated, completely consumed in the development of a single individual to the pupal stage. The typical appearance of a grain in which a single pupa of *R. dominica* was found is shown in fig. 1. Probably no more than one-third of the kernel has been eaten. A groove of increasing depth extends from the point of larval entry, round the edge of the kernel to the pupation chamber. The germ is

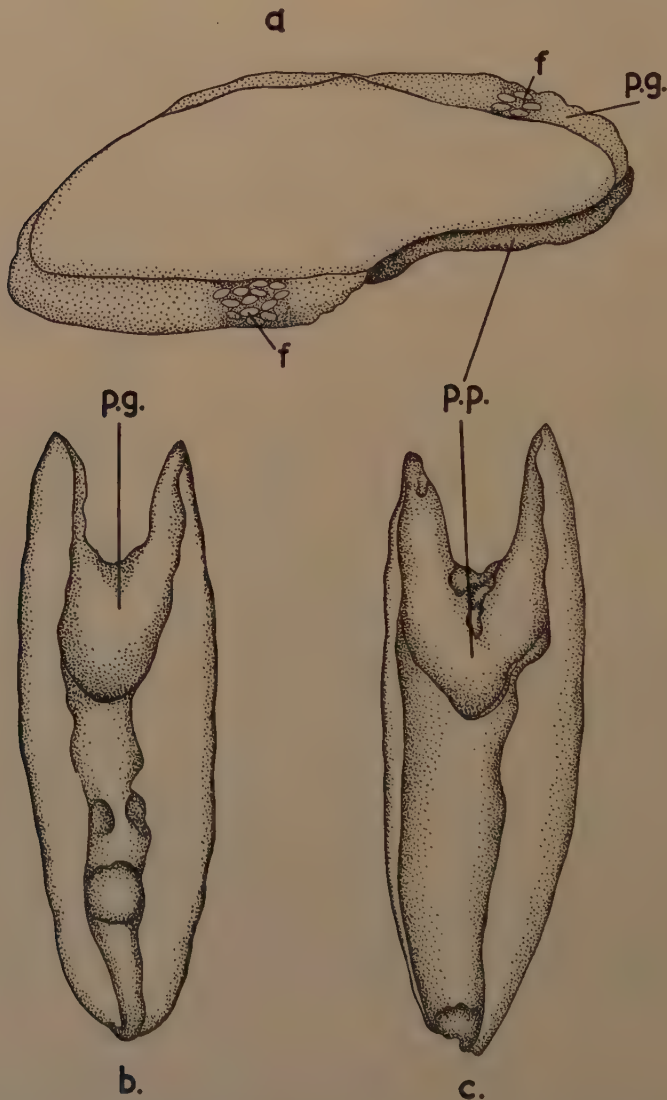


Fig. 1.—Kernel of paddy grain in which *R. dominica* had developed to the pupal stage. a, kernel as removed from husk with frass in position; b and c, kernel with grooves cleared of frass; f, detailed appearance of frass; p.g., position of germ; p.p., position of pupa.

usually eaten out. The groove is packed tight with frass, most of which consists of ovoid granules of apparently undigested endosperm mixed with a much finer floury part. This frass forms a compact mass that normally remains in position when the husk is carefully removed. When the adult has emerged there is a large irregular hole in the husk, generally situated laterally and most often near the junction of the lemma and palea. Around the hole, on the inside of the husk, is a larger scarified area. Scarification may also be found at several points on the inside of the lemma or palea, over the groove in the kernel, and it results in a weakening and often a consequent splitting of the husk of grains infested by *Rhyzopertha*. Photographs of paddy damaged by this pest are given by Hall (*op. cit.*).

(b) *Sitophilus sasakii*.—The larva hatching from an egg laid in the kernel of a paddy grain bores at random in the endosperm, but rarely perforates the pericarp. As it bores, the larva packs the tunnel behind it with a white floury frass. Pupation usually takes place in a cell lying close beneath the pericarp. The newly emerged adult can perforate the husk to some extent (see below) but usually leaves the grain by way of the same defect in the husk through which an egg was laid in the kernel. Occasionally this husk defect, although wide enough to permit oviposition in the kernel, is not apparently wide enough to allow the adult to leave the grain and it is therefore trapped within it.

(c) *Sitotroga cerealella*.—The emergence hole in the husk is smaller than that of *R. dominica* and more neatly circular (Hall, *op. cit.*), and the small flap cut out of the husk may remain attached. Normally the only obvious perforation of the pericarp is immediately below the emergence hole and there is very rarely any internal scarification of the husk. Up to two-thirds of the kernel, including the germ, may be consumed to form an irregular cavity which is for the most part packed with a white frass intermediate in texture between that of *Rhyzopertha* and *Sitophilus* and not made up of ovoid granules. The pupal case may often be found within the grain.

(d) *Lophocateres pusillus*.—Damage varies according to where the egg is laid but is usually confined to the germ and the adjacent endosperm. As with *Rhyzopertha*, a groove often extends around the edge of the kernel, but it is much shallower, generally amounting to a little more than a scarification of the pericarp. No exit hole is cut, the adult being able to emerge through the narrow slit in the husk through which the egg was laid. There are two characteristic features of attack by *Lophocateres*, viz., the frass, which is quite distinct, being made up of elongated twisted 'sausages', and the larval 'tail' segments which are found mixed with the frass, generally in the germ region.

Categories of infested grain.

Incompletely developed grain.

The grain is flattened, pale in colour, and the husk is loose and often slightly gaping. The kernel does not fill the husk and has a shrivelled appearance and a wrinkled pericarp. Its colour may be chalky-white, light green or brownish, and in consistency it may be cheesy or chalky. Hogan, Larkin & McMasters (1954) give excellent X-ray photographs of such a grain.

Immature or 'green' grain.

The colour of a sound mature paddy grain is a golden buff and the kernel is full and rounded with only a very slightly wrinkled pericarp. In contrast, the husk colour of a grain that is harvested before it is fully mature is tinged with green and the kernel may have several longitudinal ridges. The pericarp is usually more wrinkled and may also be slightly greenish or brownish; the endosperm is often chalky or brittle.

Lemma and palea separated on one side only (fig. 2).

In these grains the kernel is slightly exposed on one side owing to a separation of the lemma and palea. Jodon (in personal communication, 1958) compares the condition to that of a zip-fastener that fails to catch for a portion of its length. He believes that it is probably a varietal characteristic, though influenced by growing conditions, and he selects against it in rice breeding.

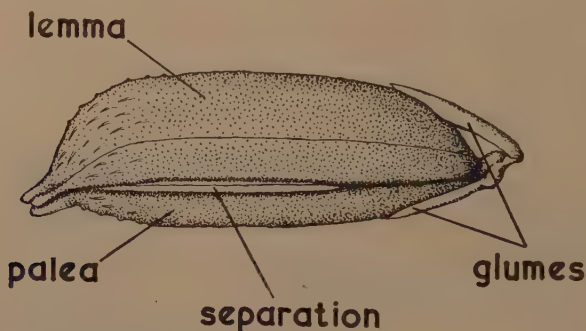


Fig. 2.—Paddy grain showing a separation of the lemma and palea on one side only.

Lemma and palea gaping.

These are grains in which the husk has failed to close properly after blooming. The kernel, which may be deformed, is exposed at the tip.

Husk cracked or split.

Any grain in which the lemma or palea is broken in any way, regardless of the size of the split or whether the break has occurred at the site of previous fungus damage, is included under the head of 'split husk'.

Germinated.

Slow-maturing paddy varieties, such as are grown in the West Indies and British Guiana, have a low germination at harvest and for about a month after. When, however, grains are immersed in water or mud, due to lodging, a few may germinate on the spikelet. On subsequent harvesting and threshing, the young plumule and radicle generally break off, leaving a hole in the lemma above the germ.

Examination of infested paddy samples.

The samples were first thoroughly sieved to remove adult insects. Repeated sievings are necessary if a reasonably accurate estimate of infestation by *R. dominica* is to be obtained. The adults remain within the grains and are not stimulated to emerge by disturbance as are the adults of *Sitophilus*. Samples were therefore sieved repeatedly over three days before a final count of adults was made. After sieving, the sample was thoroughly mixed in a Boerner sampler and 500 g. weighed out. The thousand-grain weight of the varieties Sughandi, D110 and D52/37 is approximately 30 g. at between 13 and 14 per cent. moisture. If, therefore, 500 g. of good paddy is progressively halved by four passes through a Boerner sampler, the last two 'cuts' weigh about 31 g. A further 'cut' would give approximately 15.5 g. or about 500 grains. Actual counts of grains were made

from final 'cuts' by arranging the grain in five rows and taking 50 grains at random from each row in succession, until the full total had been obtained. The grains were then placed in a 250 ml. beaker and sufficient magnesium sulphate solution poured over them to give one inch of fluid above the surface of the submerged grain. After thoroughly swirling the solution and 'bobbing' all floating grains, the floaters were skimmed off. They were then washed in tap water, dried and examined for infestation. Before any grain was dissected, notes on the husk condition, as determined by microscopic examination, were made.

The first samples of infested paddy to be examined were Trinidad-grown and of the varieties Sughandi, D110 and D52/37. The storage history and amount of each variety in store were not identical, but all had been harvested between five and five-and-a-half months when the samples, which weighed approximately 5 lb.,

TABLE I.

Classification of grains attacked by *Rhyzopertha* in samples of Sughandi, D110 and D52/37.

Sample	Live adults sieved from 5 lb.	Number of grains of different classes in a sample of 1,500 grains																Totals
		Grains with exit holes				Grains without exit holes												
		No insect	Adults (A)	Pupae (P)	Larvae (L)	Husk appar- ently good			La.* and Pa.* separ- ated or gaping			Split husk			Ger- minated			
						A	P	L	A	P	L	A	P	L	A	P	L	
Sughandi ..	2	4	2	0	1	0	0	0	3	1	3	2	2	5	0	0	1	24
D110 ..	10	2	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	5
D52/37 ..	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Totals ..		6	3	1	1	0	1	0	3	1	3	2	2	5	0	0	1	29
Grand Total		11				1			7			9			1			

* La. = Lemma, Pa. = Palea.

were taken. Sieving indicated that no sample was heavily infested with *R. dominica*, but Sughandi showed a medium infestation and D110 a very heavy infestation of *Sitophilus*. Infestation by live adults per 5 lb. of paddy for *R. dominica* was: Sughandi, 2; D110, 10; D52/37, 1; and for *Sitophilus*: Sughandi, 40; D110, 285; D52/37, 0. A sub-sample of 1,500 grains of each variety was tested by flotation and although the number of floaters was: Sughandi, 297; D110, 256; D52/37, 266, only 58 grains in all were infested. The number and classes of grains infested by *R. dominica* and *Sitophilus* are shown in Tables I and II, respectively. As stated above, there is a tendency for the husk of paddy grains infested by *Rhyzopertha* to split, and thus any original husk defect may be obscured. For this reason, no attempt was made to classify grains showing emergence holes of *R. dominica*. The original condition of most grains attacked by *Sitophilus* can, however, be determined even when the adult has emerged. The tables show that although the number of live adults of *Sitophilus* in 5 lb. of paddy was over seven times as high in D110 as in Sughandi, the total per 1,500 of grains

containing living stages of this insect was higher in Sughandi than in D110. Similarly, although only two live adults of *R. dominica* were sieved from 5 lb. of Sughandi as against 10 from the same quantity of D110, there were more grains of Sughandi containing larval stages of *Rhyzopertha* than of D110. This suggests that, at the time of sampling, breeding in both species was taking place more rapidly in Sughandi than in D110. Among the factors that might be suggested as being responsible for this is the possibility that most infestible grains had already been exploited in D110. The following observations may be made in connexion with Tables I and II:

In all but one of the grains that contained immature stages of *R. dominica*, or adults that have not yet cut an exit hole, there is a husk defect. One pupa was, however, found in a grain which apparently had a completely intact husk, suggesting that the larva is able to enter such grains, and the point of entry is not easily detected by low-power microscopic examination. No stage of *Sitophilus* was found in a grain with an apparently perfect husk, but all forms of husk defect were exploited, especially splits and separations of the lemma and palea. The infestation by *R. dominica* in the samples was too low to give a clear indication of the type of grain that is normally infested by this pest. Samples were, therefore, obtained from a British Guiana mill where high infestations by *Rhyzopertha* are known to occur. These samples were small, weighing between $1\frac{1}{2}$ and 2 lb.; seven were of D110 and two of D52/37. They were kept in the laboratory until very high infestations by *R. dominica* had developed, and, when sieved immediately before flotation, the number of live adults per lb. varied between 66 and 203 (see Table III). *Sitophilus* was also present, but not in such numbers as *R. dominica* (see Table IV). Because of the high infestations it was thought sufficient to float sub-samples of 1,000 grains. The results are given in Tables III and IV. As regards *R. dominica*, the picture presented is very different from that in Table I. In all samples, between 80 and 100 per cent. of the grains classed as infested by *Rhyzopertha* had an exit hole in the husk and were devoid of kernel or contained only small fragments (less than one-third of the original kernel). Many of these grains, even those completely devoid of kernel, contained an adult. In D110 (1) more than half of the perforated grains with small kernel fragments contained an adult, and, of the total of 165 such grains from the nine samples, 23 (13.9%) contained adults. These figures, together with the fact that no grain with an exit hole was found to have more than half of the kernel intact, indicate that when infestations are high, grains from which adults emerge are rapidly exploited by others. Larvae also enter such grains but it is a matter for speculation whether, in competition with adults for food, they would be able to complete their development. Despite the high infestation with adults of *Rhyzopertha*, the number of grains 'primarily' infested with pre-adult stages was low. There could be several reasons for this:

(1) *Shortage of food for adults*.—Birch (1945a) has shown that even with a highly infestible grain like wheat, in the absence of broken grain on which the adults can feed, *R. dominica* lays eggs at only one-eighth of its 'normal' rate. If adults of this beetle are unable to feed readily on sound grains, then when grains in which the kernel is for any reason exposed are exhausted, oviposition may be expected to fall rapidly.

(2) *Destruction of eggs*.—Schwardt (1933) has pointed out that the fragile eggs are frequently broken by the adults during or soon after deposition. Although, in paddy, eggs are commonly laid in protected situations, such as beneath the glumes or between grains and accumulations of frass, when the adult population is high the movement of beetles through the grain mass would inevitably destroy many.

(3) *Inability of larvae to enter grain*.—Birch (1945a) has stated that (in wheat) under any combination of temperature and moisture, a large proportion of the

TABLE III.
Classification of grains attacked by *Rhizopertha* in samples of D110 and D52/37.

Sample	Live adults per lb.	Number of grains of different classes in a sample of 1,000 grains												Total										
		Grains with exit holes								Grains without exit holes														
		Completely empty				<1/3rd kernel				Husk apparently good			La. and Pa. separated or gaping			Split husk			Germinated					
		No insect	A	P	L	NI	A	P	L	A	P	L	A		P	L	A	P	L	A	P	L		
D110	(1)	6	1	0	0	0	0	0	0	25	13	0	1	0	0	0	0	0	0	0	2	0	0	48
	(2)	2	0	0	0	0	0	0	0	9	2	0	1	0	0	0	0	0	0	0	0	0	0	14
	(3)	2	1	0	0	0	0	0	0	20	3	0	1	0	0	0	0	0	0	0	0	0	0	28
	(4)	2	1	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0	0	0	0	25
	(5)	3	0	0	0	0	0	0	0	14	1	0	1	0	0	0	0	0	0	0	0	0	0	19
	(6)	6	0	0	0	0	0	0	0	14	4	0	1	1	0	0	2	1	0	0	2	0	0	31
	(7)	9	0	0	0	0	0	0	0	6	0	0	0	0	1	0	0	0	0	0	0	0	0	17
D52/37	(1)	4	2	0	0	0	0	0	0	14	0	0	1	0	0	0	0	1	1	1	0	0	0	24
	(2)	2	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	14
Totals		36	5	0	0	0	0	0	0	136	23	0	6	1	0	1	2	2	2	5	0	0	0	220
Grand Total			41				165				2			3			9			0				

first-stage larvae dies without entering the grain. Also, many of those that succeed in entering both damaged and undamaged grains die in the first instar, the hazards of entering the grain apparently weakening them. One newly-emerged adult and one larva were, however, found in grains that had an apparently perfect husk.

The data shown in Table IV again suggests that infestation by *Sitophilus* is confined to paddy grains in which the kernel is for any reason exposed, or to those from which adults of *Rhyzopertha* or *Sitotroga* have emerged.

Although this aspect has not been studied, there must be some degree of competition between *R. dominica* and *Sitophilus* in mixed infestations, and the true position of the former as a pest of paddy has probably been obscured in the samples studied. The opportunity was therefore taken to make a more intensive study of paddy having an apparently pure infestation of *R. dominica*. This was in a small stock of bagged Trinidad paddy which had been in store for 5½ months, and from which a spiked sample weighing 2¼ lb. was obtained. The population of live adults as estimated by several sievings was 111 per lb. From the initial sample a sub-sample of 6,000 grains was floated twice, with an interval of 21 days between flotations. Grains containing very small larvae at the first flotation were separated out at the second. Floaters without exit holes were examined first and because these indicated a high infestation in incompletely developed grains, an attempt was made to sort out from among grains with exit holes those that were probably incompletely developed when harvested.

The analysis of infested grains is given in Table V. Of the 189 grains that were infested or had been infested with *R. dominica*, 85 (45%) were classed as incompletely developed and a further eight were classed as green. Thus almost half of the infested grains were not mature at harvest. There was a high proportion of such grains in the sub-sample as a whole. Of the 6,000 grains tested by flotation, 1,452 (24.2%) floated and the floaters were classified as follows: infested, 189; incompletely developed, 777; green, 428; 'pecky'*, 9; smut*, 23; split husk, 3; apparently good and mature, 23. Nearly 13 per cent. of all grains were incompletely developed and a further 7 per cent. were green, so that, in the paddy considered here, one grain in five was not mature when harvested. In the comparative scarcity of split-husk grains, *R. dominica* seems to have bred readily in immature grains. Infestation was again found in grains in which no defect of the husk was detected and the adult or larva of *R. dominica* was only discovered when the grain was dissected.

From the study of these natural infestations a reasonable indication of the type of paddy grain most readily attacked by *Sitophilus* and *R. dominica* was obtained. No infestation by *Sitophilus* was found in any grain with an intact husk, but larvae of *R. dominica* are apparently able to gain access to the kernels of such grains. For a female of *Sitophilus* to oviposit in any grain, it is necessary for it to be able to bore the hole in which the egg will be laid. Feeding is therefore virtually inseparable from oviposition in *Sitophilus*. Eggs are occasionally laid loose, but the apodous larva is quite unable to feed on an intact paddy grain. Thus if the intact husk of a paddy grain prevents *Sitophilus* from feeding it will also protect the grain from becoming infested with this pest. This is not necessarily so in *Rhyzopertha* because the egg is normally laid outside the grain and entry into it effected by the first-instar larva. However, the difficulty with which this is achieved has already been discussed and also the lowering of the oviposition rate in the absence of broken grains on which the adult can feed. Oviposition may be further reduced by the absence of suitable oviposition sites. Crombie (1941) has shown that, for oviposition, *Rhyzopertha* prefers rough surfaces to smooth and has a strong liking for crevices. Similarly Birch (1945a) has stated that very few eggs

* 'Pecky'—grains damaged in the field by Pentatomid bugs.
Smut—grains attacked by *Neovossia horrida*.

TABLE IV.
Classification of grains attacked by *Sitophilus* in samples of D110 and D52/37.

Sample	Live adults per lb.	Number of grains of different classes in a sample of 1,000 grains															Totals	
		Husk apparently good			Split husk			La. and Pa. separated on one side only			La. and Pa. gapping at tip			Attacked by <i>Rhyzopertha</i> or <i>Sitotroga</i>				
		A	P	L	NI	A	P	L	NI	A	P	L	NI	A	P	L		
D110	(1)	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	2	4
	(2)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	
	(3)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	
	(4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
	(5)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	(6)	0	0	0	0	1 ^{1t}	0	1	0	0	0	0	0	1	0	0	4	
	(7)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	5	
D52/37	(1)	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	6
	(2)	0	0	0	1	1	0	1	0	2	0	0	0	1+1 ^{1t}	0	0	1	8
	Totals	0	0	0	2	4	0	6	0	3	0	0	1	4	3	1	4	31

^{1t} signifies dead adult, trapped in grain.

are laid loose, the favourite site in wheat being the cracks in damaged grain. In sound wheat grains, eggs are deposited in the crease or under the loose testa. The unhulled rice grain is extremely rough, but, when sound, may lack the type of crevice favoured by *R. dominica* for oviposition.

TABLE V.

Classification of infested grains of D110 paddy infested with *R. dominica* only.

Variety	Live adults per lb.	Number of grains of different classes in a sample of 6,000 grains														
		Grains with exit holes								Grains without exit holes						
		Completely without kernel				< One-third kernel				Husk apparently good	Incompletely developed	Green	La. and Pa. separated or gaping	Split husk	Germinated	Total
		Mature		Incompletely developed		Mature		Incompletely developed								
		No insect	With living stage	No insect	With living stage	No insect	With living stage	No insect	With living stage							
D110	111	46	11	17	5	8	3	17	5	7	41	8	8	13	0	189
		57		22		11		22								

Development of *Sitophilus sasakii* in paddy samples of different infestibility (at 25°C. and 75 per cent. R.H.).

If, as indicated from the survey of natural infestations, *Sitophilus* oviposits mainly in grains with damaged husks, then the development of infestation in a given sample of paddy should be in proportion to the percentage of such grains in the sample. Estimates of the percentage of split-husk grains were made in small samples of newly harvested Sughandi, D110 and D52/37 and found to be: Sughandi, 11.6; D110, 1.5; D52/37, 0.9. The number of grains in 25 g. of these varieties would be between 750 and 825 and the number of split-husk grains as follows: Sughandi, 87 to 96; D110, 11 to 12; D52/37, 7 to 8. The paddy was conditioned to 13.5 per cent. moisture content and three 25-g. samples of each variety were used. The oviposition of young (approximately 21-day-old) mated females of *S. sasakii* was tested by placing them individually in small tubes with a single grain of milled rice and noting the number of eggs laid in two 2-day and two 3-day periods, the grain being changed at each count. Those showing an even oviposition rate, and laying 23 to 25 eggs in 10 days, were selected. Two females were placed on 25 g. grain. This is equivalent to a high infestation of about 36 females (say 72 adults) per lb. The females were removed after 10 days, and the grain left for one month before being examined for infestation. The number of adults emerging from the replicates of each variety over 30 days is shown in Table VI. A small second generation developed in Sughandi, but not in the other varieties. When the emergence of this second generation had ceased (80 days after the first adults were found) the grain samples were examined microscopically, and infested and split-husk grain separated out. It was found that infestation was

confined to split-husk grains and occurred mainly in those in which the split gaped widely. Despite this however, some adults had been unable to emerge from the grain and, as indicated in Table VI, the emergence of others had been greatly delayed. The information obtained is summarised in Table VII and shows how infestation was related to the number of split-husk grains in a sample.

TABLE VI.

Emergence of adults from 25-g. samples of paddy exposed to two females of *Sitophilus sasakii* for 10 days.

Days after removal of females	31	33	35	37	39	42	44	48	52	56	61	Total
Development period (days)	31-41	33-43	35-45	37-47	39-49	42-52	44-54	48-58	52-62	56-66	61-71	
Sughandi (1)	5	9	6	6	1	4	1	2	1	1	0	36
(2)	6	3	5	4	1	1	0	2	0	0	0	22
(3)	6	5	9	4	2	0	0	0	0	0	0	26
Total	17	17	20	14	4	5	1	4	1	1	0	84
D110 (1)	0	1	1	0	0	0	0	0	0	0	0	2
(2)	0	0	0	0	0	0	0	0	0	0	0	0
(3)	0	0	1	0	0	0	0	0	0	0	0	1
Total	0	1	2	0	0	0	0	0	0	0	0	3
D52/37 (1)	0	0	0	0	0	0	0	0	0			0
(2)	0	0	0	0	0	0	0	0	0			0
(3)	2	0	1	1	1	0	1	0				6
Total	2	0	1	1	1	0	1					6

TABLE VII.

Comparison of the number of adults of *S. sasakii* developing in 25-g. samples of paddy with different numbers of split-husk grains.

Variety	No. of split grains	No. of grains infested	No. of adults 1st gen.	No. of adults 2nd gen.	No. of adults unable to emerge	Total adults	No. of grains with two adults
Sughandi 1	99	39	36	5	0	41	2
2	84	19	22	0	0	22	3
3	94	29	26	3	2	31	2
D110 1	10	1	2	0	0	2	1
2	15	(1)	0	0	0	0	0
3	11	3+(1)	1	0	2	3	0
D52/37 1	8	0	0	0	0	0	0
2	2	0	0	0	0	0	0
3	18	6	6	0	0	6	0

Development of infestation of *Sitophilus sasakii* in sound paddy of high moisture content.

Although females of *S. sasakii* appear to select paddy grains with split husks for feeding and oviposition at normal storage moisture contents (*ca.* 14 per cent. in the West Indies and British Guiana) the possibility of feeding and breeding in sound paddy of higher moisture content has not been excluded. Experiments were therefore carried out to test the survival and breeding of the weevil in sound grain in equilibrium with relative humidities of 75, 84.3 and 92.5 per cent., at a constant temperature of 25°C.

Weevils emerging in the same 2-day period were matured for seven days in groups of 20–25 on about 15 g. milled rice. They were sexed on the seventh day and kept as individual pairs for a further three days. The oviposition of individual females was then observed over a 10-day period as before. Five selected females were placed with four males on 100 sound grains of paddy in a 3" × 1" tube closed with a muslin-covered bored cork. Three varieties of Trinidad-grown paddy, *viz.*, Sughandi, D110 and D52/37, were used and there were five replicates of 100 grains in each variety. Preliminary experiments at 75 per cent. R.H., in which the grain was examined daily, indicated that weevils began to die four days after the beginning of the experiment and that most were dead after 10 days. Males died earlier than females and in both sexes the heaviest individuals survived longest. In the actual experiments, the results of which are summarised in Table VIII, only the control tubes were examined daily; those containing grain were examined at three- to four-day intervals and on the day that all weevils in the control tubes were dead. The control tubes contained only a small piece of folded filter paper on which the weevils could rest. At no humidity was there a significant difference between survivals in grain and in the controls, indicating that all weevils died of starvation. At 75 per cent. R.H. few weevils lived for more than 12 days and males died more quickly than females. These findings are in agreement with those of Richards (1944) for the resistance to starvation of what he terms the 'small strain' of *Sitophilus oryzae*. At the higher humidities, weevils survived for longer, and there were indications of the reversal of the relative resistance of the sexes to starvation. When all the weevils were dead, the grains were microscopically examined for evidence of feeding and then kept under controlled conditions for two months to check for adult emergences. No adults emerged from any replicate, and at 75 per cent. R.H. there was no evidence of feeding on the grain apart from occasional small perforations in the glumes. At the higher humidities, however, exceptional survivals in certain replicates suggested feeding, and the grains in these tubes were therefore re-examined, during the course of the experiment, for husk defects. Six such grains were found, five in Sughandi and one in D110. At 84.3 per cent. R.H., tube no. 4 in Sughandi and tube no. 1 in D110 each contained one defective grain and at 92.5 per cent. R.H. tubes nos. 2 and 3 in Sughandi each contained two defective grains. In Sughandi no. 4, a grain 9 mm. in length was split for a distance of 6 mm. along the ridge of the lemma and for 1.5 mm. along the ridge of the palea. At its widest point, near the tip of the grain, the width of the gape was 0.4 mm. Feeding had occurred immediately beneath the split and about one quarter of the kernel had been consumed, but no eggs were laid in the grain. The edges of the split 'sutured' perfectly and there was no evidence that it was due to insect feeding. In D110 no. 1 there was a small hole about 1 mm. in diameter in one side of the lemma through which feeding on the kernel had occurred. It was impossible to determine whether or not this hole had been caused by a weevil. Of the four defective grains in Sughandi nos. 2 and 3, two were split at the extreme tip and two near the stalk. In only three were the splits sufficiently large to have allowed some feeding on the kernel, and in all splits the edges matched, indicating that they were probably due to mechanical damage. The feeding that occurred in the split grains is reflected in

TABLE VIII.
Number of adults of *Sitophilus* surviving in samples of paddy with intact husks in equilibrium with 75, 84.3 and 92.5 per cent. R.H.

R.H.	Variety	Days after beginning of experiment																					
		5	6	7	8	9	10	11	2	13	14	15	16	17	18	20	22	24	26	28	30	32	34
75%	Sughandi				6				1	1	1	1	0										
	D110				18				1	0	0	0	0										
	D52/37				3				1	0	0	0											
	Control				18				1	0	0	0											
					6				0	0	0	0											
84.3%	Percentage of all beetles dead				15				1	0													
			20	16	21	6	4	1	0	0													
		25	25			17	10	5	0														
	Sughandi				50				98.7														
				28					97														
92.5%	Percentage of all beetles dead				28																		
				10					4		3			2	1	0	0						
				19					9		6			2	2	2	0						
	D110			17					4		1			0	0	0	0						
	D52/37			18					7		1			0	0	0	0						
	Control			15					6		2			0	0	0	0						
				21					9		5			3	3	0							
		20	20	20	20	18	13	10	6	3	2	2	2	0	0	0							
		24	22	20	20	20	17	12	10	5	2	0	0	0	0								
	Percentage of all beetles dead				22.5				75		90												
	Sughandi				22.0				65		86												
	D110				20				16														
	D52/37				25				18														
					20				19														
	Control				25				18														
				20					13														
				20					20														
				25					13														
	Percentage of all beetles dead				25				24														
	Sughandi				20				16														
				18					13														
	D110			25					20														
	D52/37			20					19														
					25					18													
	Control			20					13														
				20					20														
				18					13														
			25						20														
	Percentage of all beetles dead				2.5				31														
				1					24														
									31														

The total number of adults subjected to each treatment was 20♂♂ and 25♀♀.

the better survival which is shown for Sughandi at 84.3 and 92.5 per cent. in Table VIII. These grains were replaced when discovered, and, apart from them, no feeding other than minor perforations of the glumes occurred in any grain, and no breeding took place in any variety or at any humidity. The occurrence of these husk defects in microscopically examined grains underlines the difficulty of detecting small splits when large numbers of grains have to be selected. Particularly difficult to detect are splits that occur along the ridge of the lemma or palea. In subsequent experiments, therefore, all grains were doubly checked for husk defects and smaller numbers were used.

Experiments to test the infestibility of different types of paddy grains.

In these experiments, selected females of *S. sasakii* were confined individually in small tubes with a single paddy grain. In the 'selection' tests, females of *S. sasakii* sometimes laid as many as 11 or 12 eggs in a single grain of milled rice in a 2-day period although the grain was loose in the tube. Coombs (1956) has, however, demonstrated the preference of *S. granarius* (L.) for laying in grains that are fixed. In all experiments described below, the grain was glued with a good-quality vegetable glue, to the bottom of a 5 ml. tube which was plugged with cotton-wool. Females selected for use had an even oviposition rate and laid approximately the same number of eggs in 10 days. All experiments were conducted at 25°C. and 75 per cent. R.H.

In the examination of naturally infested paddy, the grains shown to be most commonly infested were those with broken or split husks or those in which there was some separation of the lemma and palea. Grains with a wide separation of the lemma and palea, *i.e.*, in which the husk actually gapes and exposes the tip of the kernel, are relatively rare. Preliminary tests showed that they were readily infested, and that the adult usually had no difficulty in emerging from the grain. This is as might be expected because the exposure of the kernel renders the grain little different from 'brown' (*i.e.*, hulled, but not milled) rice in which *Sitophilus* both feeds and breeds (Corbett & Pagden, 1941). Such grains were not therefore used in comparative tests. Germinated grains were not tested because of their rarity nor were grains previously attacked by *Rhizopertha* or *Sitotroga* because of the difficulty of determining, except by dissection, how much of the kernel remained. Although no incompletely developed grains were found infested in the preliminary surveys, tests were conducted with this type because of the possibility that in the absence of other infestible grain, females might bore through the apparently softer husk. The types of grains used in these infestibility tests were therefore: (A) 'standard split' grains, (B) grains with damaged husks, (C) grains with the lemma and palea separated on one side only and (D) incompletely developed grain. The definitions of these categories are as follows:

(A) 'Standard split' grains.—A 'standard' split was produced in an otherwise intact husk by placing a scalpel point obliquely across the extreme tip of a firmly held grain and pressing until the husk broke on one side. Splits joining this break, but at right angles to it, usually ran back for a short distance along the ridge of both lemma and palea. The standard split did not gape to expose the kernel, but the tip of the husk could be bent away from the break so as to allow access to the kernel.

(B) Grains with damaged husks.—These grains were common in combine-harvested paddy of the varieties D110 and no. 79, obtained from British Guiana. The extent and position of the split varied, but in the grains used there was no marked exposure of the kernel although the broken parts of the husk could be easily separated so as to allow ready access to the kernel. In as far as was possible, grains showing a similar degree of husk damage were selected.

(C) Grains with the lemma and palea separated on one side only.—The degree of separation varies considerably, but no grain in which the lemma and palea

gaped at the tip, *i.e.*, in which there was some separation on both sides, was used. This type of grain was not common in the varieties available, being rarest in Sughandi, and the proportion seldom exceeded 1 per cent. in any variety examined. They were therefore tested as reasonable numbers were accumulated, without reference to variety.

(D) *Incompletely developed grains*.—Grains estimated to be not less than 'half-full' and with a tight, undamaged husk were used.

Females were left for two days on standard split grains. If oviposition in the kernel is possible, this is sufficient time for several eggs to be laid. Females confined with a single grain will, if left longer, feed on the part of the kernel to which they have access, often destroying eggs already laid. Grains of other types were examined daily under a binocular microscope without removing them from the tubes, and examinations continued until the female died or until eggs were laid (which was usually within two days), when the female was removed. After the removal or death of the females, the grains were kept under controlled conditions for at least eight weeks, when, if no adult had emerged, they were dissected to ascertain whether infestation had occurred. The results for grains in categories A, B and D are given in Table IX. No feeding and no infestation occurred in

TABLE IX.

Infestation by *Sitophilus sasakii* and adult emergence in different types of paddy grain.

Type of grain	Variety	Numbers of grains				
		Tested	Bored by ♀	Infested	In which adults developed	From which adults emerged
Standard split	Sughandi	35	8	0	—	—
	D110	35	2	0	—	—
	D52/37	35	0	0	—	—
Damaged husks	D110	30	—	16	11	4
	No. 79	30	—	16	13	9
Incompletely developed grains	Sughandi	30	0	0	0	0
	D110	30	0	0	0	0
	D52/37	30	0	0	0	0

incompletely developed grains, and this again demonstrates the inability of the female to bore through an intact husk. In the standard split grains, females were able to feed on extreme tips of the kernels in eight grains in Sughandi and two in D110, but no infestation developed in any grain in any variety. A possible explanation for this lack of infestation despite feeding is that whereas the female could insert the rostrum through the split sufficiently to bite the extreme tip of the kernel it could not penetrate far enough to bore the type of hole in which an egg is laid. The higher proportion of bored grains in Sughandi may indicate a greater flexibility of the husk, but the number of grains used was too small to demonstrate any real varietal differences. Infestation in grains with damaged husks was surprisingly low, amounting to just over half of the number exposed; and about half of the adults that developed were unable to leave the grain.

The results for grains with a separation of the lemma and palea on one side are given in Table X. As already stated, this type of grain was not common and in those available the separation was usually narrow. In almost half of the grains

used it measured less than 0.11 mm. at the widest point. If the width of the separation exceeded 0.3 mm., the lemma and palea usually gaped at the tip. Females were rarely able to bore into the kernel when the separation measured less than 0.11 mm. With separations between 0.11 and 0.17 mm. wide it again appeared as if the rostrum could not be pushed in far enough to allow a hole to be bored sufficiently deep to accommodate an egg. Adults were able to emerge from only half of the grains in which they developed. Emergence involves the paring away of one or both of the husk components at the separation, or sometimes the cutting of a definite exit hole. *S. sasakii* is therefore able to perforate the husk when working from the inside outwards, but the siliceous epidermis of the husk

TABLE X.

Infestation by *Sitophilus sasakii* and adult emergence in grains with lemma and palea separation on one side only.

	Width of lemma and palea separation in millimetres							Total
	<0.11	>0.11- 0.14	>0.14- 0.17	>0.17- 0.20	>0.20- 0.23	>0.23- 0.26	>0.26- 0.30	
Numbers of grains	73	32	17	11	20	6	4	163
Numbers bored by ♀	4	18	10	11	18	6	4	71
Numbers infested	2	12	4	9	17	5	4	52
Numbers in which adults developed	1	10	4	9	14	5	4	47
Numbers from which adults emerged	1	3	3	4	8	3	2	24

and the hard, 'glassy' hairs which are abundant on its outer surface probably protect the grain from external attack. Occasionally the adult would succeed in getting its head and thorax out of the grain and then become trapped. The placing of more paddy in the tube would sometimes give the adult sufficient purchase to enable it to crawl out of the grain, but most trapped adults died. There were eight grains in which two adults developed, but from only two of these did both adults emerge. In four, both adults failed to leave the grain, and in two one adult emerged and one died. In Table X the last two are included among the grains from which adults emerged.

Infestibility of sound paddy by *Rhyzopertha dominica*.

Experiments similar to those conducted with *Sitophilus sasakii* on survival and breeding in sound paddy in equilibrium with relative humidities of 75, 84.3 and 92.5 per cent. were carried out with *Rhyzopertha dominica* at a temperature of 29.4°C.

Adults emerging over a 14-day period from well-sieved cultures were used and these were sexed by examination of the genitalia. Beetles were lightly narcotised with ether, and the genitalia exerted by pressing on the abdominal sternites with a curved Borradaile needle. If this is done with care no harm appears to result to either sex. After sexing, individual pairs were kept separately on bruised wheat for four to seven days before being used. Birch (1945a) states that females begin to lay eggs within the first few days of their emergence from the grain and, if plenty of food is available, the maximum rate of oviposition is reached in the first 14 days. Provided they had paired, therefore, all females used should have been ready to lay eggs at the beginning of the experiment. Five 100-grain replicates of each of the varieties Sughandi, D110 and D52/37 were used at each

relative humidity. The inner faces of the bored corks of the 3" x 1" tubes were protected from possible adult boring by being covered with a well-fitting disc of plastic gauze. The control tubes at 75 per cent. R.H. each contained a folded piece of filter paper and a filter-paper disc covered the bottom of the tube. The latter was considered necessary because adults of *R. dominica* are almost helpless on glass and expend a great deal of energy attempting to walk on it. At 84.3 and 92.5 per cent. R.H., plastic gauze was substituted for filter paper in both cases. Four males and five females were used in each tube.

In order to avoid the possibility of injury to eggs and especially to young larvae, it was decided to limit examinations of the grain to the fifth day after the beginning of the experiment and to when all beetles in the controls were dead. The first examination was before any eggs had hatched and gave an indication of whether oviposition was taking place and whether there was any marked adult mortality within the first five days. At the second examination it was possible to compare mortality in the controls and in the grain and to obtain an indication of whether the beetles in sound paddy were dying of starvation. In the meantime, the tubes were examined regularly, without disturbing their contents, for signs of frass (or grain dust). This is a sure indication that the adults are able to bore into the grain and in infestible cereals like wheat it is produced in large quantities even by a few individuals. If, however, no obvious adult feeding is taking place, the presence of frass may be taken to indicate that adults have developed within the grain, and are beginning to cut exit holes. The results are condensed to give Table XI. The use of filter paper in the control tubes at 75 per cent. R.H. was unfortunate, but was made before reference to Crombie (1941) was possible. This author showed that adults of *R. dominica* survived for 20 to 44 days on Whatman's No. 1 filter paper, *i.e.*, considerably longer than on 'food' substances such as salted peanuts, ground soya beans and dried milk. It soon became apparent that adults were biting the edges of the filter paper and tending to attack it gregariously at certain points. The total amount of filter paper 'consumed' when all control beetles were dead was, however, exceedingly small. Examination of the grain five days after the start of the experiment revealed eggs in D110 and D52/37, but none were found in Sughandi. Evidence of the adults having fed on the glumes was seen in each variety. On the 25th day after the start of the experiment, frass was being ejected from one grain in Sughandi. This grain was extracted from the tube and examined microscopically. A small split, the edges of which sutured perfectly, extended from the extreme tip of the grain back along the ridge of the lemma for a distance of 1 mm. On one side at the tip, the lemma was loose from the palea and so could be lifted away from the kernel. This grain was kept separately under the conditions of the experiment and a lightly pigmented adult emerged after a further ten days. Forty-four days after the beginning of the experiment, frass ejection was noted from two more grains in Sughandi. Since by this time all but one of the control adults were dead it was decided to re-examine the grain, but no infested or split-husk grains were found in the other varieties. Of the two found in Sughandi (tubes nos. 2 and 5), one had a minute split (1 mm.) at the extreme tip of the lemma. Hatched eggs just within the split indicated that infestation had begun at this point. The grain contained a fully pigmented adult which was beginning to cut a small hole in the palea near the tip. The ejection of frass was taking place through this hole. In the second grain, the extreme tip of the palea had been broken off and there was a split measuring 0.5 mm. at the tip of the lemma. A groove of increasing depth extended from the tip of the kernel along the upper edge to the germ where a fully pigmented adult was found. This adult had cut a small hole in the lemma immediately above the germ and was ejecting frass through it. There was no evidence of adult penetration nor of infestation in any other grains, but between 12 and 17 per cent. of the glumes showed various degrees of feeding. No females were alive in any

tube, but two males still survived. The grain was kept for a further eight weeks at the humidity and temperature of the experiment, but no other adults emerged and there was no further frass ejection. One of the surviving males died 54 days after the start of the experiment and the other three days later.

It was evident that of the 1,500 grains used in this experiment, three had had minute splits in the husk from the beginning, and oviposition or larval penetration had occurred in these. Feeding or infestation had apparently not been possible in the remainder.

Unlike *Sitophilus sasakii*, *Rhyzopertha dominica* appeared less resistant to starvation at the higher humidities, and, at 92.5 per cent. R.H., most control beetles were dead ten days after the beginning of the experiment. At each humidity, males survived longer than females both in the controls and on grain. Evidence of some oviposition by the fifth day, but none of direct feeding on the grain, was found in each variety at 84.3 and 92.5 per cent. R.H. At 84.3 per cent., seven grains (five in Sughandi and two in D52/37) became infested, infestation being indicated by the appearance of frass in the tubes. Microscopic examination of these grains revealed that each one had a small husk defect. These defects were in the nature of true splits of the lemma or palea which must have been present at the beginning of the experiment. No split exceeded 3 mm. in length and four were less than 1.5 mm. long. Infestation was first noticed 37 days after the beginning of the experiment, by which time three adults had developed. The ejection of frass from the grain probably begins as soon as the adult starts to cut an exit hole in the husk. No other infestation developed in any variety and no grain was found that had been bored into by an adult, although the proportion of grains with damaged glumes was much higher than at 75 per cent. R.H. Two grains, both with minute splits (less than 1 mm. long) at the tip of the lemma, became infested at 92.5 per cent. R.H. They were both discovered, one in Sughandi and one in D110, 29 days after the beginning of the experiment when one contained two fully pigmented adults that were beginning to cut exit holes in the husk. No evidence of adult feeding, other than on the glumes, was found in any grain.

As with *Sitophilus*, subsequent experiments were conducted with individual grains that were doubly checked for husk defects.

Experiments with different types of paddy grain exposed individually to single females of *Rhyzopertha dominica*.

The conditions obtaining with regard to an individual grain in a bulk are as follows: (a) The grain is fairly stable, being surrounded and held in place by others, (b) the intergranular space amounts to some 40 per cent. of the total volume and provides sufficient space for adults and larvae to move through the bulk, (c) neighbouring grains provide a rough and stable surface against which adults or larvae can obtain a purchase when attempting to bite or enter the grain, (d) the intergranular atmosphere is usually in equilibrium with the moisture content of the grain. In experiments in which paddy grains were exposed individually to single females, these conditions were reproduced in as far as was possible by using the brick slabs described earlier. The slabs were also used in tests to select 'guaranteed layers'. Barnes & Grove (1916) showed that in the oviposition cycle of *R. dominica*, periods of active egg-production alternated with periods of increased feeding during which fewer eggs were laid. Tests were not continued long enough to confirm this observation, but it was noticed that females which did not bore actively into the test wheat grain rarely laid many eggs. Since it was desired in experiments to test not only the oviposition of a female on a given grain but also its ability to attack that grain, females selected had shown a high egg-production and marked boring activity over a given period. Individual females, drawn at random from stock cultures, were confined in 'cells' in the

slabs with a single grain of wheat, the tip of which had been cut off at the germ end. Oviposition was observed over three 2-day periods, the females being transferred to new grain at each count. As many as 40 eggs were occasionally laid in a 2-day period, and an average of 10 eggs a day was common. Females were left on the test paddy grains for two days. If left longer than this they tended to destroy some of the eggs already laid, especially if these had been placed beneath the glumes. Two days was considered long enough for a female to display any ability to bore into a given grain because with wheat grains an hour was sufficient for a marked depression to be cut into the surface.

Grains were examined for infestation 14 days after the female had been removed. This is long enough for infestation to develop and to be easily detectable, but not so long that the point of entry of the larva into the grain is likely to be obscured. At this examination, oviposition, which could be checked to some extent when females were removed, was confirmed and details of feeding, on the

TABLE XII.

Feeding, oviposition and infestation by *R. dominica* in different types of paddy grain.

Type of grain	Variety	Numbers of grains					Total live infestation
		Tested	Bored by adult	Oviposition confirmed	Infested		
					via rachis	not via rachis	
Intact husk and glumes	Sughandi	30	0	23	0	1	1
	D110	30	0	23	0	0	0
	D52/37	30	1	18	0	1	1
Standard split	Sughandi	30	0	—	0	25	25
	D110	30	0	—	0	27	27
	D52/37	30	0	—	0	26	26
Green	Sughandi	30	0	27	0	0	0
	D110	30	0	21	1 (3)	1	2
	D52/37	30	0	21	0	0	0
Incompletely develop d	Sughandi	30	0	24	3 (3)	0	3
	D110	30	0	27	1	0	1
	D52/37	30	0	24	1	2	3

Figures in parentheses denote the number of grains in which a larva, having bored into the rachis, died before reaching the kernel.

grain or on the glumes, recorded. Paddy of the varieties Sughandi, D110 and D52/37 was again used, and the types of grains exposed were: mature grains with intact husks, standard split grains, green grains and incompletely developed grains. All grains used had both glumes intact so as to provide a possible oviposition site. There is one husk defect that may be concealed by the glume at the base of the lemma and that is a short split along the keel of the lemma immediately above the germ. In most paddy varieties a line of weakness, which allows the shoot to break through at germination, exists in the lemma at this point. Grains were examined for such splits before infestation was checked by dissection. All tests were made at 29.4°C. and 75 per cent. R.H. using grain and slabs equilibrated to these conditions. The results are given in Table XII. Of all the grains tested (360) only one, a mature grain with an intact husk, was attacked by a female. A neat round hole was cut in one side of the lemma and the kernel was

bored almost completely through. No eggs were noted when the female was removed from the grain, but subsequent examination revealed two larvae boring between the kernel and the husk on the side of the grain away from the initial perforation. It is probable that eggs had been laid in the cavity bored by the female. One other grain with an intact husk was found on dissection to contain four larvae, but the site of initial entry into the grain was not determined.

Nearly 87 per cent. of the standard split grains became infested and dissection revealed that, in most of these, eggs had been deposited through the split against the tip of the kernel. Most grains contained more than one living larva, and one contained as many as seven. In many grains one or more larvae had penetrated to the germ.

Two green grains of the variety D110 became infested but none in Sughandi and D52/37. In both, eggs had been laid beneath the glumes and in one a single larva had reached the kernel by boring through the centre of the rachis. In the other, three larvae were feeding near the germ, but the way in which they had penetrated the husk was not found. In a further three grains of D110 a larva had bored into the rachis but had died before penetrating to the kernel.

Seven grains in all, of the 90 incompletely developed grains tested, became infested and, of these, five showed that the larva had reached the kernel by boring through the centre of the rachis. In the other two grains, the kernel had first been fed upon at the extreme tip and it seemed probable that the larvae (four in each grain) had managed to penetrate between the lemma and palea at the tip of the husk. In an incompletely developed grain the attachment between the lemma and palea is far less secure than in a full one and although all grains in which there was any indication of a gape were rejected, there is no doubt that a separation of the husk components, especially at the tip, is much easier in incompletely developed grains than in those that are full and mature. There were again three grains in which a larva, having bored into the rachis, died before reaching the kernel.

Experiments in which six eggs of *Rhyzopertha dominica* were placed with individual grains of different types of paddy of the varieties Sughandi, D110 and D52/37.

In the previous experiment, eggs had been laid against the kernel in most grains with a husk defect, and in all grains where eggs had been so placed an infestation had resulted. With grains in which there was no husk defect, eggs had either been laid loose in the cell or beneath the glumes. Although there was only one instance of an adult succeeding in perforating the husk and attacking the kernel of any type of grain, most grains (72 per cent. of all tested) showed evidence of feeding having taken place upon the glumes. In a few, the swollen indurated bases of the glumes had been bitten through completely and the glumes detached, and, in others, feeding had also taken place on the base of the rachis. In feeding on the glumes, adults would often destroy eggs that had been laid beneath them, and some of the eggs laid loose in the cells were also destroyed by the movements of the adults. There was, therefore, variation in the number of eggs that escaped damage with different types of grain and with individual grains of a given type. In order to eliminate this variation and to find out whether infestation could occur with equal ease when eggs were laid loosely outside the grain, the experiment was repeated but, instead of females being confined with grains in cells, six eggs were placed with each individual grain. The eggs had been laid by females being tested individually on single wheat grains, and had been allowed to incubate for three to five days. Only eggs showing the changes indicative of normal embryonic development were used.

Grains were dissected for infestation 14 days after the eggs had been placed with them and at the same time a check on the viability of the eggs was made.

In most cells all eggs hatched; there were only two instances (both with incompletely developed grain) of the six eggs failing to hatch. The results (Table XIII) are comparable with those obtained when females were confined individually with single grains.

No grain with an intact husk was infested in any variety, but infestation developed in all but one of the standard split grains. Of the grains that were green or incompletely developed, no more than two out of 30 became infested in any variety. The total number of grains infested in these two categories was ten, and in eight of these larval entry was by way of the rachis. In the remaining two, the indications were again that the larvae (two in each grain) found within the husk had penetrated between the lemma and palea at the tip of the grain.

TABLE XIII.

Infestation developing in different types of paddy grains when six eggs of *R. dominica* are placed with individual grains.

Type of grain	Variety	Numbers of grains			Total live infestation
		Tested	Infested		
			<i>via rachis</i>	not <i>via rachis</i>	
Intact husk and glumes	Sughandi	30	0	0	0
	D110	30	0	0	0
	D52/37	30	0	0	0
Standard split	Sughandi	30	—	30	30
	D110	30	—	30	30
	D52/37	30	—	29	29
Green	Sughandi	30	1	0	1
	D110	30	2 (3)	0	2
	D52/37	30	2 (2)	0	2
Incompletely developed	Sughandi	30	2 (1)	0	2
	D110	30	1 (3)	1	2
	D52/37	30	0 (1)	1	1

Figures in parentheses denote the number of grains in which a larva, having bored into the rachis, died before reaching the kernel.

It is of interest to point out here that in both this and the previous experiment, when infestation had taken place by way of the rachis, only a single larva was found within the husk, but when the way of entry was thought to be between the tips of the lemma and palea two or more larvae were found. Furthermore, in both experiments at least half the larvae that bored into the rachis died without reaching the kernel. This suggests that when, as is often the case in an incompletely developed grain, the lemma and palea are slack and tend to separate at the tip, larvae of *R. dominica* have little difficulty in gaining access to the kernel. When, however, the only means of access to the kernel is by boring along the rachis, entry is usually restricted to a single larva and there is, as might be expected, a high mortality because even in wheat many larvae die when attempting to bore into undamaged grain. In the two instances (see Table XII) in the previous experiment of infestation in grains that were full and believed to have intact husks there was again more than one larva in each grain. In the mature grain there were four larvae and in the 'green' grain there were three. In both grains, feeding had started near the germ end of the kernel, suggesting a split in

the husk possibly below the lemma or palea, but unfortunately in neither grain was this found.

These two experiments point clearly to the extent to which larvae of *R. dominica* can utilise even minute husk defects in order to gain access to the kernel of a paddy grain. Larvae may also enter the husks of 'green' or incompletely developed grains by boring along the rachis, but this method of entry involves a high mortality and such grains are in consequence much less infestible than those with husk defects.

Discussion and conclusions.

These investigations have underlined the difficulties involved in dealing with any but small quantities of grain when studying the infestibility of paddy. The aim has therefore been to determine the infestibility of an individual type of grain under controlled conditions in experiments where the variability has been reduced as much as possible. The results of these experiments have combined to demonstrate that, with the paddy varieties used, the grain with an intact husk is immune to attack by *Sitophilus sasakii* even at high moisture contents but that any husk defect that allows the female to bite into the kernel renders the grain liable to be infested. However, in order for an adult that has developed within a grain to play its part in the multiplication of the population, it must be able to leave the grain and to pair with another of the opposite sex. That this is often not possible has been shown by the results of the experiments with infestible grains and also by the examination of infested samples of paddy. Thus, even in the early stages of an infestation, the full reproductive potential of *S. sasakii* in paddy is probably only manifest when there is a considerable choice of infestible grains. For example, in the samples of Sughandi (Table VII), females appear to have selected, for oviposition, grains in which the split in the husk gapes widely and in consequence, although the total of potentially infestible grains in 75 g. of this variety was 277, only 87 grains (31.4%) were initially infested. In these circumstances, most of the adults of the new generation are able to leave the grains in which they developed. If, on the other hand, the choice of grains becomes limited with succeeding generations, more adults are likely to develop in grains from which they will be unable to emerge. The development of high populations of *S. sasakii* in paddy, as in D110 (Table II), must therefore be an indication of a high proportion of infestible grains. The extent to which grains are reinfested is probably less with *S. sasakii* than with *Rhyzopertha dominica*. With readily infestible grains such as wheat and milled rice there is often a natural tendency for the adult of this species to remain, for some time after emergence, within the grain in which it developed. This tendency is increased when, as with paddy, exit from the grain is often difficult or even impossible. In such circumstances much of the kernel is consumed, especially in the region of the husk defect where the adult tries to cut an exit hole. This means that any other adult attempting to reinfest the grain will have difficulty in reaching the kernel with its rostrum unless it is able actually to crawl into the grain. That entry by an adult into a paddy grain is more difficult than emergence from it, was frequently demonstrated in experiments, when weevils that had successfully emerged from grains, became trapped (and eventually died) when attempting to re-enter them.

It has already been stated that feeding and the ability to infest a grain are inseparable in *S. sasakii*, but not in *R. dominica*. That the adult of the latter is also unable to feed on most grains with an intact husk has been demonstrated in the experiments carried out with this beetle. In only one grain of the 5,220 used in experiments was the husk bitten through and the kernel bored into; in general, feeding on sound paddy grains was confined to the glumes and base of the rachis. Probably no grain of the varieties used in these experiments is completely immune

to infestation by larvae of *R. dominica*. Splits and other husk defects, however small, are readily exploited, often by several larvae, but even in the absence of these the larva may gain access to the husk by way of the rachis. It was found that larvae could more easily penetrate the rachis of grains that were harvested when not fully mature. Hector (1936) has pointed out that in the great majority of cultivated types of rice the articulation of the spikelet to the pedicel is completely solidified and the spikelet on being threshed is broken off by fracture. In a mature grain the broken rachis is hard and shrunken and the pith much contracted. In a grain harvested and threshed when incompletely developed or while still green there is less contraction of the pith and therefore the larva of *R. dominica* probably finds it easier to bore along the rachis. Nevertheless, many die before reaching the kernel. The extent to which immature grains may become infested is indicated in the Trinidad sample of D110 (Table V), but the immature grain with an intact husk appears to be as resistant to attack by the feeding adult as the sound mature grain.

The general conclusion is, therefore, that the mature paddy grain with an intact husk is not infestible by *S. sasakii*, and is probably almost as immune to infestation by *R. dominica*. However, husk defects render the grain infestible by both species and especially by *R. dominica*, the larvae of which can exploit much smaller cracks than can the adults of *S. sasakii*. Similar conclusions in regard to the immunity of paddy to attack by *Sitophilus* have been reached by other workers, but they usually found that *R. dominica* could "feed and breed" in paddy if only to a limited extent. Their accounts suggest, however, that they have assumed that this difference represents a difference in the ability of the adults to attack the grain and they have ignored the possibility of there being defects in the husk which could be exploited by one insect and not the other, or to a different degree by both. P. M. Davey & I. Forsyth (unpublished report, Pest Infest. Lab., 1953), who found that *R. dominica* lived and bred on both swamp and upland paddy while *Sitophilus oryzae* died, did not examine their grain at the beginning of their experiments, and so the possibility that some of the paddy grains used had husk defects of a type that could be exploited by larvae of *R. dominica* but not by adults of *S. oryzae* cannot be excluded. Cleare (*op. cit.*), who selected his paddy grains by visual (but not microscopic) examination, found that *Sitophilus* sp. and *R. dominica* caused a similar degree of damage over a similar time. Cleare inferred from this that at a moisture content of between 14 and 15 per cent. these two beetles were equally capable of attacking "sound" paddy. In the experiments described above, grains were examined microscopically and yet some with husk splits sufficiently wide to allow feeding and oviposition by *S. sasakii* were overlooked. It is possible therefore that the degree of damage reported by Cleare represents the proportion of split-husk grains that existed in his selected paddy.

Prevett's (1959a, b) results probably provide the most convincing confirmation of the importance of husk defects in regard to the infestibility of paddy by *Sitophilus* and *R. dominica*, although this author makes no reference to this factor. He found that *Sitophilus* was unable to live or breed in stored raw paddy (*i.e.*, paddy not parboiled) but could live and breed in parboiled paddy. *R. dominica* survived and bred on a sample (made up of several varieties) of raw paddy, but not nearly to the same extent as on parboiled paddy. In infestibility tests with 19 different varieties of raw paddy, Prevett found that *R. dominica* was able to breed to a limited extent in 16 of them, but the highest number of adults that he obtained in the F₁ generation from 1,000 grains of any variety was ten as against 123 from parboiled paddy. It is of particular interest to note that two of the varieties shown to be slightly infestible in these variety tests had been incorporated in the "mixed" raw paddy sample used in the raw *v.* parboiled paddy infestibility experiment. Prevett considered that the husk gave support to the first-instar

larva of *R. dominica* during its initial penetration into the kernel, hence the greater infestibility of parboiled paddy as compared with milled rice, but he did not suggest reasons for the differences in infestibility of parboiled and raw paddy. The greater infestibility of parboiled paddy is undoubtedly due to the tendency for the lemma and palea to separate during parboiling, especially when the process is somewhat crude, as it is in the region of Sierra Leone where Prevett conducted his experiments. The kernel of the parboiled paddy grain when dried to, say, 14 per cent. moisture differs little in volume from that of the raw paddy grain at the same moisture content, but the husk components once separated by the swelling of the kernel, do not again close fully on drying. Consequently, parboiled paddy tends to be slightly bulkier than raw paddy. Prevett found that a standard volume of raw paddy weighed 280 g. as against 250 g. for parboiled paddy. The greater infestibility of parboiled paddy is therefore a reflection of the proportion of grains with the lemma and palea so separated that larvae of *R. dominica* can gain access to the kernel.

The rapid multiplication of a population of *R. dominica* in paddy is dependent not only on a high proportion of infestible grains, but also on an adequacy of food in the form of split-husk grains, hulled grains and kernel fragments. Immature paddy, while being infestible in a greater degree than mature grain, does not initially provide conditions under which a greater number of eggs will be laid. Until a new generation of adults has emerged and there are kernel fragments available for feeding, the rate of development of the infestation will be slow. Hand-harvested paddy appears, in the main, to contain a low proportion of infestible grains and little food material. The paddy used by Prevett was all hand-harvested and, as stated above, showed a low infestibility by *R. dominica* until parboiled. Similarly, J. R. Tuckett (A report on an investigation into the methods of drying and storing rice adopted by peasant cultivators in the St. Augustine-Streatham Lodge district (Trinidad).—Unpublished D.T.A. report, Imp. Coll. trop. Agric., Trinidad, 1954) reported negligible infestation, even after several months' storage, in Trinidad peasant paddy that had been harvested and threshed by hand. G. Stell (personal communication, 1959), on the other hand, reported eventual infestations by both *S. sasakii* and *R. dominica* in mechanically threshed Trinidad paddy into which BHC dust had been mixed before storage. It seems, therefore, that although certain varietal characteristics such as the failure of the husk to close properly around the kernel may render a small proportion of the paddy infestible by *Sitophilus* or *Rhyzopertha*, infestibility is, for the most part, induced during harvesting or threshing. In this connection it is interesting to examine the proportion of infestible grains and kernel fragments in samples of British Guiana paddy. In this country the peasant method of threshing paddy is known as 'bull-mashing,' i.e., bullocks are walked over heaps of reaped rice until the grain is separated from the straw. A fair proportion of the paddy is however reaped and threshed by combine harvester. In Table XIV the number of split-husk grains in 30 g. (approx. 1,000 grains) in nine samples of bull-mashed paddy is compared with that in ten samples of paddy threshed by combine harvester. All samples were newly harvested and free of infestation. The weight and number of pieces of hulled grain per 30 g. gives an indication of the degree of splitting of the husk. The more extensive the breakage of the husk, the more likely is the kernel to break and be separated out from the husk. The average number of split-husk grains in combine-harvested paddy is 115 and that in bull-mashed paddy 75; this difference is highly significant ($P > 0.01$). The greater extent of fragmentation of grains in combine-harvested paddy is even more striking. Compared with an average of 41 pieces of hulled grain per 30 g. in combine-harvested paddy, there are on average only about 5 pieces in 30 g. of bull-mashed paddy.

The combine-harvested paddy therefore provides not only an average of more

than 10 per cent. grains of which the husks are fairly extensively split but also some 620 pieces per lb. of hulled grain (of average weight 9.5 mg.) on which adults of *R. dominica* can feed. In such circumstances the full laying capacity of this pest can probably be exercised even at the beginning of the infestation, and high populations quickly built up. Cleare (*op. cit.*) has given some indication of the infestation by *R. dominica* in the paddy milled at a large mill in British Guiana which handles mainly combine-harvested rice. In 'monitor chits', i.e., the small pieces of hulled rice removed by the monitor from the paddy before it is parboiled, he found 140 live adults of *R. dominica* per ounce. Some 600 lb. of monitor chits are produced a day and, on a daily milling capacity of about

TABLE XIV.

Split-husk grains and hulled grain in samples of combine-harvested and bull-mashed paddy.

Variety	How harvested	Split-husk grains/30 g.	Wt. of hulled grain/30 g. (in g.)	No. of pieces of hulled grain/30 g.	Av. wt. of broken pieces (in mg.)
1 No. 79	Combine	152	0.808	82	9.85
2 No. 79	Combine	143	0.811	80	10.1
3 D110	Combine	75	0.32	31	10.3
13 D110	Combine	93	0.33	38	8.69
14 D110	Combine	92	0.187	18	10.4
15 No. 79	Combine	90	0.360	39	9.23
16 D110	Combine	86	0.250	22	11.36
17 D110	Combine	116	0.299	31	9.65
18 No. 79	Combine	79	0.075	9	8.33
19 No. 79	Combine	224	0.450	63	7.15
Average ..		115	0.39	41	9.50
4 No. 79	Bull-mashed	45	0.066	8	8.25
5 No. 79	Bull-mashed	52	0.105	10	10.5
6 No. 79	Bull-mashed	60	0.059	6	9.8
7 Mixed	Bull-mashed	63	none	0	0
8 Mixed	Bull-mashed	35	0.002	2	0.75
9 Mixed	Bull-mashed	191	0.084	12	7.00
10 Mixed	Bull-mashed	48	0.048	4	12.08
11 Mixed	Bull-mashed	112	0.049	5	9.8
12 Demerara Creole	Bull-mashed	71	0.027	3	8.93
Average ..		75	0.049	5.5	7.45

168,000 lb. of paddy, this represents an over-all infestation of eight adults of *R. dominica* per pound. This figure is, however, based only on live beetles removed by the monitor. Many adults would probably have been removed in the scalperators and cyclones through which the paddy passes before entering the monitor, and others may have been killed by the BHC powder with which the monitor chits were admixed. In an earlier section, reference has been made to the necessity for repeated sievings over several days if a true estimate of the number of adults of *R. dominica* in paddy is to be obtained, and it is probable that the actual infestation in the paddy is considerably higher than Cleare's figures would indicate.

In addition to having a higher proportion of split and hulled grains, combine-harvested paddy often contains more green grains than paddy which is harvested

by hand. The varieties at present grown in British Guiana show a marked photo-periodicity, and very little variation in ripening dates can be achieved by varying planting dates. Much of the combine harvesting is done on contract and where there is a demand on the machines it is inevitable that some paddy must be harvested a little early. Furthermore, all the paddy in a field is usually harvested at one time. When harvesting is done by hand, it is possible to leave for a few days later-ripening patches of low-lying paddy, but the contractor operating a combine harvester is unable to do this, and rice that is not quite mature is harvested with the rest.

The combine harvesting of any grain creates a drying problem and this may be acute in British Guiana where humidities are high and the weather is often changeable during the harvest seasons. Hall (*op. cit.*) has drawn attention to the inadequacy and paucity of the drying facilities in many British Guiana mills, and Cleare states that although a moisture content of 14 per cent. is aimed at for stored paddy, much is taken into storage with a moisture content of 16 per cent. or more. When such high moisture contents obtain in paddy having about 10 per cent. grains with badly split husks, a varying proportion of green grains, and in which there are many pieces of hulled grain, conditions are favourable for the development of both *Sitophilus oryzae* and *Rhyzopertha dominica*, and it is suggested that it is the combination of these factors that makes possible the high infestations seen in stored paddy in many British Guiana mills.

Summary.

Indications of the type of paddy grain most commonly infested by *Sitophilus sasakii* (Tak.) and *Rhyzopertha dominica* (F.) have been obtained from the examination of infested samples of paddy grown in Trinidad, W.I., and in British Guiana.

Small-scale experiments with sound mature paddy have shown that *S. sasakii* is unable to feed and breed in a grain with an intact husk, even when the moisture content is high. It is also probable that *R. dominica* finds it extremely difficult to attack and infest such grains.

The rapid multiplication of *S. sasakii* in paddy is dependent on there being a high proportion of grains with badly damaged husks. Infestation can occur in grains with a slight separation of the lemma and palea, or with slightly split husks, but the adult that develops is often unable to emerge from such grains.

Larvae of *R. dominica* readily make use of even minute husk defects in order to gain access to the kernel of a paddy grain. Entry of the larva into the husk may also be effected by boring along the centre of the rachis and this is easier in incompletely developed and green grains than in those that are full and mature, but entry by this method is usually restricted to a single larva and the mortality is high.

The degree of husk damage and the amount of hulled and broken grains in paddy may often be related to the method of harvesting and threshing. In British Guiana, combine-harvested paddy generally has a much higher proportion of damaged grains than paddy harvested and threshed by traditional peasant methods. When combine-harvested paddy is stored at a high moisture content, conditions may be favourable for the development of high infestations of *S. sasakii* and *R. dominica*.

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References.

- APT, A. C. (1952). A rapid method of examining wheat samples for infestation.—*Mill. Prod.* **17** p. 4.
- BALZER, A. I. (1942). Insect pests of stored rice and their control.—*Fmrs' Bull. U.S. Dep. Agric.* no. 1906, 22 pp.
- BARNES, J. H. & GROVE, A. J. (1916). The insects attacking stored wheat in the Punjab and the methods of combating them, including a chapter on the chemistry of respiration.—*Mem. Dep. Agric. India (Chem. Ser.)* **4** pp. 165–280d.
- BIRCH, L. C. (1945a). A contribution to the ecology of *Calandra oryzae* L. and *Rhizopertha dominica* Fab. (Coleoptera) in stored wheat.—*Trans. roy. Soc. S. Aust.* **69** pp. 140–149.
- BIRCH, L. C. (1945b). The influence of temperature on the development of the different stages of *Calandra oryzae* L. and *Rhizopertha dominica* Fab. (Coleoptera).—*Aust. J. exp. Biol. med. Sci.* **23** pp. 29–35.
- BREESE, M. H. (1955). Hysteresis in the hygroscopic equilibria of rough rice at 25°C.—*Cereal Chem.* **32** pp. 481–487.
- CHEO, Ming-tsang & CHANG, Yun-hwa (1943). Studies on the rice weevil (*Calandra oryzae* L., Coleoptera). Control (1). [*In Chinese with English summary.*]—*New agric. J., Yungan* **3** pp. 178–216. Rept. as *Tech. Bull. Fukien prov. Coll. Agric.* no. 23, 39 pp.
- CHITTENDEN, F. H. (1916). The Siamese grain beetle (*Lophocateres pusillus* Klug.).—*Bull. U.S. Bur. Ent.* no. 96 pp. 14–18.
- COPELAND, E. B. (1924). Rice.—352 pp. London, Macmillan.
- COOMBS, C. W. (1956). Stability of grain as a factor influencing the oviposition rate of the grain weevil, *Calandra granaria* (L.) (Col. Curculionidae).—*Bull. ent. Res.* **47** pp. 737–740.
- CORBETT, G. H. & PAGDEN, H. T. (1941). A review of some recent entomological investigations and observations.—*Malay agric. J.* **29** pp. 347–375.
- CROMBIE, A. C. (1941). On oviposition, olfactory conditioning and host selection in *Rhizopertha dominica* Fab. (Insecta, Coleoptera).—*J. exp. Biol.* **18** pp. 62–79.
- DOUGLAS, C. E. [1925]. Rice—its cultivation and preparation.—147 pp. London, Pitman.

- DOUGLAS, W. A. (1941). Field infestation by insects that injure rice in storage.—*Circ. U.S. Dep. Agric.* no. 602, 8 pp.
- FLOYD, E. H. & NEWSOM, L. D. (1959). Biological study of the rice weevil complex.—*Ann. ent. Soc. Amer.* **52** pp. 687–695.
- GHOSE, R. L. M., GHATGE, M. B. & SUBRAHMANYAN, V. (1956). Rice in India.—507 pp. New Delhi, Indian Coun. agric. Res.
- HECTOR, J. M. (1936). Introduction to the botany of field crops. Vol. 1 (Cereals).—478 pp. Johannesburg, Centr. News Agency.
- HOGAN, J. T., LARKIN, R. A. & McMASTERS, M. M. (1954). X-ray and photomicrographic examination of rice.—*J. agric. Fd Chem.* **2** pp. 1235–1239.
- PREVETT, P. F. (1959a). A study of rice storage under tropical conditions.—*J. agric. Engng Res.* **4** pp. 243–254.
- PREVETT, P. F. (1959b). An investigation into storage problems of rice in Sierra Leone.—*Colon. Res. Stud.* no. 28, 52 pp.
- RICHARDS, O. W. (1944). The two strains of the rice weevil, *Calandra oryzae* (L.) (Coleopt. Curculionidae).—*Trans. R. ent. Soc. Lond.* **94** pp. 187–200.
- ROUSE, P., ROLSTON, L. H. & LINCOLN, C. (1958). Insects in farm-stored rice.—*Bull. Ark. agric. Exp. Sta.* no. 600, 25 pp.
- SCHWARDT, H. H. (1933). Life history of the lesser grain borer.—*J. Kans. ent. Soc.* **6** pp. 61–66.
- STOKES, R. H. & ROBINSON, R. A. (1949). Standard solutions for humidity control at 25°C.—*Industr. Engng Chem.* **41** p. 2013. -

THE EFFECT OF REPEATED INSECTICIDAL APPLICATIONS ON A NATURAL TSETSE POPULATION.

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Recently Simpson (1958) has presented a theoretical examination of the effect of introducing sterile males into an isolated population of tsetse flies (*Glossina* spp.). The problem was treated mathematically by a technique due to Leslie (1945), in which the expected number of females in each age-group is considered in detail. The calculations were based upon data derived from the life-cycle of the fly, and were carried out on the electronic computer at Rothamsted, England.

The effect of repeated applications of a non-persistent insecticide is, mathematically, a very similar problem. It has been tackled arithmetically (G. F. Burnett, unpublished report), but the method was lengthy and laborious, only a few examples were dealt with, and simplifying assumptions had to be made to keep the arithmetic to manageable proportions. A mathematical model of the problem was therefore set up from which a suitable programme was prepared for the electronic computer.

It should perhaps be emphasised that an insect population varies in a complex manner, and that any mathematical model must of necessity contain assumptions that do not hold exactly, so that figures derived from it cannot be regarded as exact predictions. Such models can give useful general information, however, and often lead to a more rational approach to a particular problem.

The mathematical model.

First it is necessary to set up a model for a natural population. If subscripts r, n refer to age and time respectively, in weeks, age being measured from the time of pupation of the larva, let

$v_{r,n}$ be the expected number of females in the age-group $(r, r+1)$ alive at time n ;

$\pi_{r,n}$ be the probability that a female of this age-group, alive at time n , is still alive at time $n+1$;

$\phi_{r,n}$ be the expected number of female pupae, deposited in the time interval $(n, n+1)$ by a female of this age-group, which is still alive at time $n+1$.

Then the age structure of the female population at time n may be represented by the vector

$$v_n = (v_{0,n}, v_{1,n}, v_{2,n}, \dots, v_{r,n}, \dots)$$

and the elements of the corresponding vector at time $n+1$ are given by

$$v_{0,n+1} = \sum_{r=0}^{\infty} \phi_{r,n} v_{r,n} \quad (1)$$

i.e., the expected number of female pupae up to a week old at time $n+1$ is the sum of the expected number of females of each age-group multiplied by the

expected number of female pupae deposited by a female of that age-group; and

$$v_{r+1,n+1} = \pi_{r,n} v_{r,n} \quad (2)$$

i.e., the expected number of females in the age-group $(r+1, r+2)$ at time $n+1$ is the expected number of females in the age-group $(r, r+1)$ alive at time n , multiplied by the probability of survival.

From assumptions about the life-cycle of the flies in a natural population, explicit values can be derived for v , π , and ϕ . Full details are given by Simpson (*op. cit.*); it is assumed that the undisturbed population would have been stable, so that the age vector v remains constant, and the biological aspect of this and other assumptions will be discussed later in this paper.

To examine the effect of repeated insecticidal applications, it is assumed that an application uniformly and instantaneously reduces the number of adult females to a fraction k of its pre-treatment level, i.e., the age vector

$$v_n = (v_{0,n}, v_{1,n}, v_{2,n}, \dots, v_{r,n}, \dots)$$

is replaced by

$$v'_n = (v_{0,n}, v_{1,n}, \dots, kv_{a,n}, kv_{a+1,n}, \dots, kv_{r,n}, \dots)$$

where a is the pupal period in weeks. Using equations (1) and (2), the age vectors at times 1, 2 . . . can then be calculated successively; some time after the last application they converge to a constant fraction of the original age vector. It is assumed in the theory that π and ϕ are essentially unaltered by the insecticidal applications.

The life-cycle of the tsetse fly.

It is worth while enumerating the biological significance of some of the assumptions made in setting up the mathematical model.

- (i) To assume that the undisturbed population would have remained constant is to assume that births and deaths would have been nearly equal over the period of time considered in the calculations.
- (ii) If π and ϕ are essentially unaltered by the applications, then the only effect of the insecticide is to kill a proportion of the adult females at specified times. At other times, females in the treated population have exactly the same probability of survival as those in a natural and untreated population, and produce pupae in the same way. Thus, for example, no density-limiting factors can act upon the population as it declines, and the production of pupae by the females is independent of the population level.
- (iii) Death is a random process in which the probability that a fly will die in a short time interval is proportional to the length of the interval and is independent of the age of the fly.
- (iv) Male and female pupae are equi-probable.

Every natural tsetse population fluctuates in size, sometimes violently, but it is considered that the assumption of near-equality in births and deaths will not greatly affect the validity of general conclusions drawn from the theory. It is not proved that there are no density-limiting factors acting upon tsetse populations, but there is good evidence in work by Hocking and others (Hocking, Yeo & Anstey, 1954; Hocking, Burnett & Sell, 1954; Hocking & Yeo, 1956) that such factors, if they do exist, act very slowly even upon populations greatly reduced by insecticidal applications, and that the population dynamics of such reduced populations are very similar to those of the original populations; there is, however, a lower limit, probably of a few flies per square mile, to the density of a self-perpetuating population, below which the flies soon die out in an area. As for the equi-probability of male and female pupae, Jackson (1949) states that "workers too numerous to mention have established that the sexes emerge in

equal or nearly equal numbers". Numerous quantitative studies of population numbers using marked flies (for example, Jackson, 1948), suggests that in nature the incidence of death is at random, or at least approximately so.

Data summarised by Jackson (1949) and Buxton (1955) show that the life-cycle of the tsetse fly varies very considerably under field conditions. If all the parameters involved in the numerical calculations were positively correlated so that they changed by the same proportionate amounts, there would be need to change only the basic time unit for the results to be widely applicable. In fact, although the parameters, such as expectation of life, pupal period, and the periods between production of larvae, are usually positively correlated, the correlations are not simple. The following values were chosen as reasonable averages for savannah species such as *Glossina morsitans* Westw. living in East Africa during the dry season:—

- (i) Pupal period of females = 4 weeks
- (ii) Expectation of life of females = 6 weeks
- (iii) Each adult female produces her first larva three weeks after emergence, and subsequent ones at intervals of one-and-a-half weeks.

Calculations were then made for various values of k , the proportion of adult females surviving each application; i , the interval in weeks between successive applications; and t , the number of applications.

Results.

The calculations covered all combinations of

$$t = 1, 2, \dots, 8$$

$$k = 0.05, 0.10, \dots, 0.50$$

$$i = 1, 2, \dots, 6, \text{ and also the case of } i \text{ so large } (\gg 6) \text{ that the population has time to become stable between applications.}$$

TABLE I.

The stable levels of the residual populations, expressed as percentages of the original level, for k values of 0.05 and 0.50.

t i	1	2	3	4	5	6	7	8
$k=0.05$								
1	36.12	25.53	17.25	9.05	.86	.06	.005	.001
2	36.12	18.14	1.81	.31	.13	.02	.002	.0004
3	36.12	10.75	1.30	.41	.11	.02	.004	.001
4	36.12	5.07	.96	.14	.03	.004	.001	.0001
5	36.12	6.78	1.17	.26	.05	.009	.002	.0003
6	36.12	9.71	2.10	.50	.11	.03	.006	.001
$\gg 6$	36.12	13.05	4.71	1.70	.61	.22	.08	.03
$k=0.50$								
1	66.38	47.52	35.02	25.19	16.49	10.31	6.38	4.06
2	66.38	45.47	29.11	18.42	11.90	7.76	5.01	3.22
3	66.38	43.42	27.71	18.10	11.78	7.63	4.95	3.21
4	66.38	41.85	26.76	17.00	10.85	6.91	4.40	2.80
5	66.38	42.32	27.34	17.60	11.33	7.29	4.69	3.02
6	66.38	43.14	27.95	18.15	11.78	7.64	4.96	3.22
$\gg 6$	66.38	44.06	29.24	19.41	12.88	8.55	5.68	3.77

k = proportion of adult females surviving an application.

t = number of applications.

i = interval in weeks between applications.

Full details of the calculations have been deposited with the British Museum (Natural History); some results are given in Table I, which gives values of the final stable populations, expressed as percentages of the original population, for the extreme values of k considered in the calculations.

Table I and the other results show that four weeks is always the most effective of the intervals considered and gives the lowest residual population for a given series of applications; an interval of five weeks is the next most effective. The least reductions in population for a given series of applications are obtained with an interval of one week, or else a very large number of weeks, between successive applications. Varying the interval between applications has least effect when k is large; thus, with eight applications and $k=0.50$, the residual population varies only between 2.80 per cent. and 4.06 per cent. for all values of the interval, whereas it varies from 0.0001 per cent. to 0.03 per cent. for the same values of the interval when $k = 0.05$.

The stable residual populations for different values of k are summarised in Table II for the most effective interval between applications ($i=4$ weeks).

TABLE II.

The stable levels of the residual populations, expressed as percentages of the original level, for an interval of four weeks between successive applications.

k t	0.05	0.10	0.15	0.20	0.25	0.30	0.35	0.40	0.45	0.50
1	36.12	39.48	42.84	46.20	49.56	52.92	56.29	59.65	63.01	66.38
2	5.07	8.43	11.97	15.69	19.60	23.69	27.96	32.41	37.01	41.85
3	.96	2.27	3.93	5.97	8.40	11.22	14.45	18.11	22.21	26.76
4	.14	.52	1.16	2.12	3.43	5.15	7.31	9.98	13.19	17.00
5	.03	.14	.37	.79	1.45	2.41	3.75	5.51	7.88	10.85
6	.004	.03	.11	.29	.60	1.12	1.91	3.07	4.70	6.91
7	.001	.008	.04	.10	.25	.52	.98	1.70	2.80	4.40
8	.0001	.002	.01	.04	.10	.24	.50	.94	1.67	2.80

k = proportion of adult females surviving an application.

t = number of applications.

Changes in the value of k give striking differences in the levels of the residual population. Thus, four applications leave a population of only 0.14 per cent. of the original level when $k = 0.05$, while for $k = 0.50$ the corresponding figure is 17.0 per cent. An increase in the number of applications also reduces the final level considerably when k is small; thus, for $k = 0.05$, an increase from four to eight in the number of applications drops the final level of population from 0.14 per cent. to 0.0001 per cent.

Discussion.

The detailed effect of the applications is complex. For the first three weeks or so of adult life a female does not produce larvae. Almost immediately after it is deposited, the larva burrows into the ground and pupates; several weeks are spent in this stage, immune from the effect of the insecticide, before the emergence of the adult, which is vulnerable. There is thus always an appreciable proportion of the population present as pupae, and even when all available adults are killed, the applications would have to continue

for a complete pupal period for eradication to ensue. With a complete kill, the interval between applications could be extended to three weeks, and still no adult would become old enough to produce a larva.

When kills are incomplete, many of the adult females surviving the first application will be producing larvae, and the sooner the second application is made the fewer will be the pupae produced: this reasoning also applies to survivors of subsequent applications. As regards individuals present as pupae at the start of a series of applications, however, the second application will be most effective when it is delayed for a complete pupal period, because this ensures that the maximum number of adults are present; effects are greatest even though some of the emerged adults will have larviposited, because during the first pupal period emergences will be at the same rate as for the undisturbed population, whereas larviposition will inevitably be reduced.

Increasing the interval between the first and second applications thus increases the adult proportion of the population at the time of the second spraying, at any rate for intervals up to one pupal period; but at some larger intervals the production of pupae, by survivors of the first application and by females that have emerged after it, reduces the adult proportion, and the effectiveness of the second application will be decreased. Thus there is an optimal interval between the first and second application, comparable in length with the pupal period or possibly slightly exceeding it, and it seems reasonable to suppose that this interval will be optimal for a series of applications.

The calculations support this general reasoning, in that a four-week interval is always most effective for given values of k and t . However, there are some curious results. For $k < 0.25$, i.e. for kills of 75 per cent. or more per application, and for four or seven applications, and also for $k < 0.45$ and eight applications, the two-weekly interval is better than the three-weekly one, and this is contrary to the general argument given above. It appears that there is some interaction between t , i and, probably, the period taken by a female to produce its first larva, which causes these apparent anomalies. Such results are relatively unimportant, however, because the differences are slight, and they do not seriously detract from the general conclusion that the most effective intervals are centred about a value equal to, or perhaps slightly greater than, the pupal period.

In a series of experiments with insecticides, Hocking and others (Hocking, Parr, Yeo & Anstey, 1953; Hocking, Yeo & Anstey, 1954; Hocking, Burnett & Sell, 1954; Hocking & Yeo, 1956) have recorded k values of the order of 0.1, and have usually carried out six to eight applications at intervals of two weeks. In some cases eradication, or near eradication, has been achieved for populations initially of the order of up to a few thousands per square mile, and this agrees reasonably well with what might have been expected from the calculations. In other cases, however, despite k values of, apparently, 0.1 or thereabouts, the residual populations have been of the order of 1 per cent., some two orders of magnitude greater than that predicted by the theoretical calculations.

No entirely satisfactory explanation has been found for this discrepancy, particularly since the small residual populations have remained low and relatively stable over periods of several years in areas where immigration was unlikely or virtually impossible, indicating the minor importance of density-limiting factors even if they exist. Burnett (unpublished) discussed the various possibilities that might explain the poorer results, among them the development of resistance to the insecticide as the applications continue, smaller kills of young flies compared with old flies leading to an overestimate of the actual kill during the later applications, and the existence of ecological niches containing the residue of the fly population when it has been greatly

reduced and in which the flies are inaccessible to the insecticide. As Burnett realised, however, these factors can be used to explain the results only if they operate in some cases and not in others, which is not a very acceptable hypothesis.

Burnett also suggested that perhaps the kill per application was grossly over-estimated in the less successful experiments. This would require true kills of females to be about 60 per cent. to fit in with the predicted results, and this is perhaps possible in view of the relatively small catches upon which the estimates of k were made. One possibility, not previously considered, is that under field conditions many pupae may take considerably longer than average to emerge as adults. For some individuals, this would mean that the probability of their being adult at the time of an application would be effectively reduced, and, when intervals between applications are relatively short, this might mean that an appreciable proportion of the population would be effectively attacked only once. Combined with an unfortunate combination of poor applications, always a possibility in East Africa, this might considerably reduce the effectiveness of a series of applications.

Thus it is not possible to relate the theoretical calculations with all the results so far obtained in the field. It does seem likely, however, that something would be gained from making the interval between successive applications four weeks rather than the two weeks or so of past experiments, since it is rare for pupal periods in East Africa to be less than 3-4 weeks during the times of the year when insecticides are normally applied. The longer interval would more nearly correspond to the optimum predicted by the calculations, and would make less likely the chance of escape by individuals whose pupal periods were much in excess of the average value. It would also mean that a single aircraft, or other machine, could tackle an area where with the shorter interval two would have been required, although, of course, the total period during which any given number of applications would be applied would be twice as great.

Summary.

Using a deterministic model of a tsetse population, theoretical calculations have been made of the effect of repeated applications of a non-persistent insecticide upon a natural population. It has been assumed that the insecticidal applications instantaneously reduce the adult population, and that there is no residual effect.

For the numerical work it has been assumed a female fly has a pupal period of four weeks and an average expectation of life of six weeks and produces her first larva three weeks after emergence, and subsequent ones at intervals of one-and-a-half weeks.

Results have been calculated for kills of females varying from 50 per cent. to 95 per cent. per application, for series of up to eight successive applications, and for intervals between successive applications of from one to six weeks and also for the case when the population is allowed to become stable between applications.

With high kills per application, very drastic reductions are to be expected from six to eight applications, and the theory predicts the best results for an interval between applications of four weeks.

An attempt is made to relate the theoretical results with those achieved in actual field experiments. The reductions in population were sometimes very much smaller than those predicted by the theory; some tentative, but not entirely satisfactory, suggestions are made to account for these anomalous results.

References.

- BUXTON, P. A. (1955). The natural history of tsetse flies.—*Mem. Lond. Sch. Hyg. Trop. Med.* no. 10, 816 pp. London, Lewis.
- HOCKING, K. S., BURNETT, G. F. & SELL, R. C. (1954). Aircraft applications of insecticides in East Africa. VIII. An experiment against the tsetse fly, *Glossina swynnertoni* Aust., in an isolated area of thorn-bush and thicket.—*Bull. ent. Res.* **45** pp. 613–622.
- HOCKING, K. S., PARR, H. C. M., YEO, D. & ANSTEY, D. (1953). Aircraft applications of insecticides in East Africa. IV. The application of coarse aerosols in savannah woodland containing the tsetse flies *Glossina morsitans* and *G. swynnertoni*.—*Bull. ent. Res.* **44** pp. 627–640.
- HOCKING, K. S. & YEO, D. (1956). Aircraft applications of insecticides in East Africa. XI. Applications of a coarse aerosol to control *Glossina morsitans* Westw. at Urambo, Tanganyika, and *G. morsitans* Westw., and *G. pallidipes* Aust. in Lango County, Uganda.—*Bull. ent. Res.* **47** pp. 631–644.
- HOCKING, K. S., YEO, D. & ANSTEY, D. G. (1954). Aircraft applications of insecticides in East Africa. VI. Applications of a coarse aerosol containing DDT to control the tsetse flies *Glossina morsitans* Westw., *Glossina swynnertoni* Aust. and *Glossina pallidipes* Aust.—*Bull. ent. Res.* **45** pp. 585–603.
- JACKSON, C. H. N. (1948). The analysis of a tsetse-fly population. III.—*Ann. Eugen.* **14** pp. 91–108.
- JACKSON, C. H. N. (1949). The biology of tsetse flies.—*Biol. Rev.* **24** pp. 174–199.
- LESLIE, P. H. (1945). On the use of matrices in certain population mathematics.—*Biometrika* **33** pp. 183–212.
- SIMPSON, H. R. (1958). The effect of sterilised males on a natural tsetse fly population.—*Biometrics* **14** pp. 159–173.

A TRIAL USE OF GRASS-MAT PASSAGES IN PROTECTING HUMANS FROM ATTACKS BY TSETSE FLIES.

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In March 1957, an outbreak of human sleeping sickness was discovered in the South Mamprussi District of northern Ghana. Medical control measures were initiated straight away, but for various reasons it was not possible to begin tsetse control measures until late in the year.

The policy adopted when these were started was to make, first of all, mile-long protective clearings of the riverine vegetation at each village in the affected area, and when this had been completed, to carry out selective clearing of the river systems in the area of the outbreak. This process was obviously going to be quite lengthy, and a start could not be made at every village at the same time. The possibilities of providing some sort of quickly achieved protection at the villages which would otherwise be left unprotected for some time seemed worth examining. This protection would have to remain effective until the permanent protective clearings could be made. Speed and cheapness were obviously mandatory, but permanency was not.

Little detailed work appears to have been published on the relative importance, in host-finding, of scent and sight in *Glossina*, but, whereas in *G. pallidipes* Aust. scent seems to be at least as important as sight (Fuller & Mossop, 1929), in *G. morsitans* Westw. and *G. swynnertoni* Aust. it appears that food is found by sight rather than by scent (Lloyd, 1935), and the same appears to be true of *G. palpalis* (R.-D.) and *G. tachinoides* Westw., which are the prevalent species of tsetse in this part of Africa. It was therefore assumed that the tsetse hunted by sight alone and the possibilities of hiding humans from view were considered. A means lay ready to hand, the tall grass, *Andropogon gayanus*, used in making grass mat (Zana mat) for hut-building, etc., had just attained its full stature.

Method.

A survey was first of all carried out to find which water-holes in the district were suitable for this technique. The points that were looked for were:—

(a) the practicability of driving stakes into the ground on either side of the path to the water-hole; (b) an even gradient along the path to the water-hole to avoid large gaps at the bottom of the mats; (c) the practicability of carrying a grass-mat screen around the place from where water was actually taken. It was not considered obligatory to be able to cross the entire stream; taking the mat out in a loop a few yards across the stream was considered to be satisfactory, but firm anchorage of the supports was of paramount importance; (d) the absence of any small vegetation-covered cliffs or knolls which would overlook the passage.

Four sites were selected on the Zangu and Salga rivers, which are tributaries of the river Nasia. In a normal season the stream is dry for most of the year, and water has to be obtained from water-holes in its bed, but at the time of the experiment the water was continuous, though it dried up soon afterwards.

The sites for the passages having been chosen, three proficient grass-mat weavers and three grass-gatherers were engaged. The mats made were about 4 ft. 6 in. in height and about 12 ft. in length, though there was a considerable variation in this respect, lengths of between 9 and 16 ft. being encountered.

The passage was designed to enclose the path to the stream and to start about 75 yd. from the water and to be about 10 ft. across, widening out to about 20 ft. at the water's edge and forming a large loop around the water-hole, leaving enough room for a party of women to wash clothes, etc. Stakes were driven in on each side of the path, and, when these had been tested for firmness, the mats were tied on in two tiers, so that the final height of the walls was about 8 ft. When the mats were carried out over the water, a space of about 1 ft. was left between the bottom of the mat and the ordinary level of the water, to allow for flooding.

Covering the top of the passage to hide the villagers from the sight of any tsetse that might be resting higher than 8 ft. above ground-level was considered, but the idea was abandoned lest snakes and scorpions should be attracted into the tunnel thus formed.

Where there was more than one water-hole at a village, the chief was asked to ensure that only the protected water-hole was used. This measure was very successful.

Cost.

About 1,100 ft. of matting was required for each passage. This took the labour force about eight days to weave and three days to put up, a total of 66 man/days per passage. Each labourer was paid 5 shillings per day.

TABLE I.

Fly-boy and trap catches of *G. palpalis*, totals per month.

Situation		Trap		Fly-boy	
		Oct.	Nov.	Nov.	Dec.
Buzulungu	Outside	46	25	376	197
	Inside	1*	0	0	12
Tempela	Outside	9	6	9	8
	Inside	2*	0	0	1

* Teneral flies.

TABLE II.

Fly-boy and trap catches of *G. tachinoides*, total per month.

Situation		Trap		Fly-boy	
		Oct.	Nov.	Nov.	Dec.
Buzulungu	Outside	0	0	37	31
	Inside	0	0	0	0
Tempela	Outside	0	0	0	0
	Inside	0	0	0	0

Results.

Catching and recording of flies, starting in October 1957, were done at only two of the villages.

At both these villages, two Morris traps were sited, one inside and one outside the passage, and were examined daily (Sundays excepted). At the beginning of November 1957, the trap system was supplemented by fly-boys catching by hand. One fly-boy was stationed at each site, spending alternate days inside and outside the matting, at the water's edge. The traps had to be withdrawn at the end of November. The monthly total numbers of individuals of *G. palpalis* and *G. tachinoides* are shown in Tables I and II, respectively.

Discussion.

It is notable that the only flies found inside the grass-mat passages in October were teneral individuals. It may be that they came from outside, but they could well have come from inside the passage itself. The site for the grass-mat passage was cleared through the original fly-belt in September, and pupae derived from any larvae deposited there before the clearing would in all probability remain undamaged in the soil to give rise to adults during October. Indirect support for this is drawn from the fly-boy and trap figures for November, where not one fly was caught inside the passage.

The apparent decline in effectiveness in December arises from the greater concentration around the water-holes of cattle and sheep, which walked through the matting. This loss in effectiveness was not serious, however, as by the time it occurred the work on protective clearings was under way at these villages.

The efficacy of the mat passages in keeping the flies out tempts one to make certain deductions on the habit of these two species of tsetse at that season (late rains and early dry season) in that type of vegetation (fringing fly-belt, mainly *Berlinia heudelotiana*, *Pterocarpus santalinoides*, *Alchornea cordifolia* and *Syzygium guineense*; up to 20 ft. in height).

First, the flies could not have been more than 8 ft. above water-level, as above that height they would presumably have seen the villagers coming down to the water. Secondly, that the 1-ft. gap between the water-level and the bottom of the mat did not lead to flies entering. It would seem that the portions of human anatomy that showed beneath the matting did not attract the fly. The third deduction was that they were not attracted by the scent of the humans within the matting passage.

In the matter of cost, the quoted figure of 66 man/days for each passage gives a total cost, in Ghana, of £16 10s. 0d. This is negligible considering the cost of making a one-mile-long protective clearing on the Zangu and Salga rivers, which worked out at £177 17s. 6d., or 711½ man/days.

It seems fair to assume, therefore, that the passages did all that was asked of them; they were effective in keeping tsetse out until the protective clearing could take over their function permanently and were cheap and quick to erect.

Summary.

In March 1957, an outbreak of human sleeping sickness was discovered in the South Mamprussi District of northern Ghana. Temporary measures were initiated at a few villages to provide protection, at water-holes on streams, against attack by the two prevalent species of tsetse, *Glossina palpalis* (R.-D.) and *G. tachinoides* Westw., until clearings could be made.

These measures consisted of grass-mat passages approximately 8 ft. high, extending from about 75 yd. from the stream down to and around the water-hole. At the water-hole, there was a gap of about 1 ft. between mat and water.

These passages were found to be successful in excluding tsetse fly. This suggests several points of interest about *G. palpalis* and *G. tachinoides*: that at that time of year and in that type of vegetation, they do not rest higher than 8 ft. above ground; that the portions of human anatomy that showed beneath the matting did not attract the fly; and that these species depend on sight for hunting rather than on smell.

The cost of this matting was negligible as compared with the cost of routine clearing, and this method of temporary protection was considered successful for its purpose.

References.

- FULLER, C. & MOSSOP, M. C. (1929). Entomological notes on *Glossina pallidipes*.
—*Bull. Dep. Agric. S. Afr.* no. 67, 27 pp.
- LLOYD, H. M. (1935). Notes on the bionomics of *Glossina swynnertoni*, Austen.
—*Bull. ent. Res.* **26** pp. 439–468.

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THE BEHAVIOUR OF THE ADULT OF *APHODIUS TASMANIAE* HOPE
(COL., SCARABAEIDAE) IN SOUTH AUSTRALIA:

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(PLATE XVII.)

Aphodius tasmaniae † Hope is an indigenous insect which has been recognised as an economic pest of improved pastures in southern Australia for about 30 years (Carne, 1956). The species is widely distributed in South Australia but is particularly prominent as a pasture pest in the lower South-East which is the largest area in the state with an assured rainfall (fig. 1).

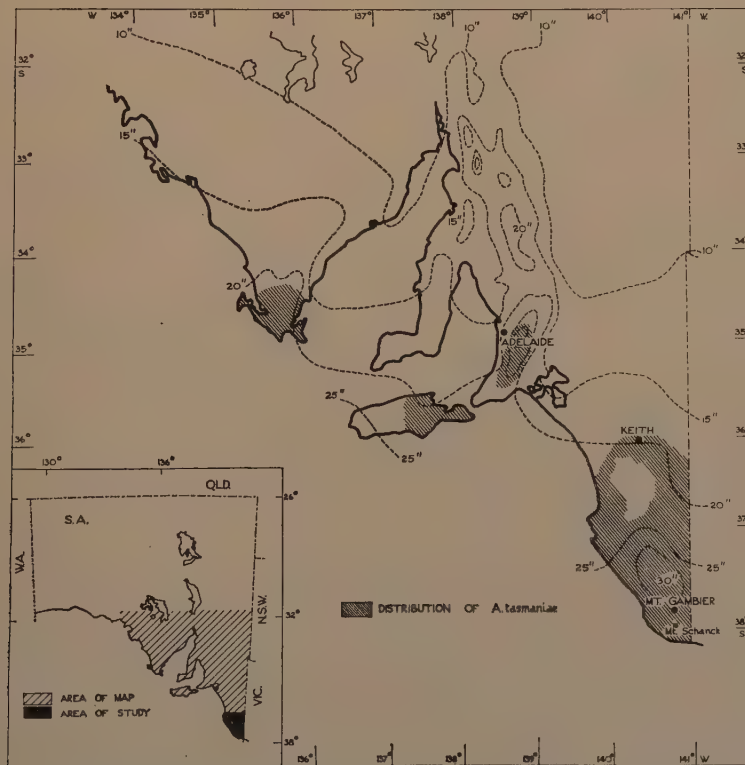


Fig. 1.—The distribution of *Aphodius tasmaniae* in South Australia in relation to mean annual rainfall in inches (after Madge, 1952). The area of study is shown in the inset.

* The work included in this paper formed part of a thesis accepted by the University of Adelaide for the Ph.D. degree.

† In recent years *A. tasmaniae* has been referred to in Australian literature as *A. howitti* Hope; the former name has page priority (Given, 1958).

There is only one generation of *A. tasmaniae* each year in South Australia, as in other parts of southern Australia. In the lower South-East (fig. 1), to which area this study was confined, the adults fly and lay their eggs in the soil during the summer period January–March. The eggs hatch in 3–4 weeks, but the first-instar larvae remain in the soil until the soil is saturated by the first substantial autumn rains. They then migrate to the surface of the soil, make individual burrows, and commence feeding, first on plant debris on the surface of the soil and then on pasture foliage. The larvae stop feeding about September, retreat to the bottom of their burrows, construct cells in the soil and enter diapause. Pupation commences in December and the adults emerge 2–3 weeks later.

The larvae of *A. tasmaniae* are commonly found to be distributed very patchily with areas of high density interspersed with extensive areas in which the density is low. A possible explanation of this type of distribution is that it results from the habit of the adults aggregating in certain areas to lay their eggs. The purpose of this study was to determine the factors which influenced the survival rate, aggregation and oviposition of the adults in the field.

Emergence, flight and oviposition.

Emergence.

After metamorphosis, the adults lie quiescent in the cells constructed by the larvae before diapause some 6–8 in. below the surface of the soil, and emerge from their cells in large numbers at particular times during summer. Analysis of flights of *A. tasmaniae* at Canberra, Australian Capital Territory, indicated that there was a significant correlation between flight and rainfall above a certain number of points (Carne, 1956). This correlation suggested that the adults of *A. tasmaniae* emerge from their cells after an increase in the moisture content of the soil, as do adults of *Lepidiota caudata* Blkb. (Smith, 1936).

A total lack of 'effective' rain in January 1955 at Mt. Gambier presented an opportunity for determining experimentally whether or not an increase in the water content of the soil stimulated the emergence of the adults of *A. tasmaniae*. A 12 ft. × 2 ft. plot in a pasture, which was known to contain large numbers of beetles, was encircled and watered with 190 gal. of water (equivalent to about 1½ in. of rain) on 25th January 1955. On the following day a number of adults within the watered plot had left their cells and were within 1–2 in. of the surface of the soil, and at dusk on 27th January a number of beetles emerged from the soil. Some of these beetles took off in flight when the wire-gauze covering the plot was removed for a few minutes. When the cover was replaced, other beetles, after attempting to fly, crawled on the surface of the soil and copulated. No beetles were caught in a light-trap on this night and intensive searching indicated that no beetles had emerged from the pasture outside the watered plot.

On 28th–31st January 1955, a reciprocal experiment was conducted, a plot being kept covered whilst rain fell. Some beetles emerged from the rest of the pasture after this rain but the beetles in the covered plot remained in their cells and only emerged when the plot was subsequently watered. These results leave little doubt that the adults are stimulated to emerge when the soil is wetted.

Beetles have subsequently been observed, on a number of occasions, to appear 'en masse' on the surface of the soil at dusk two or three days after rain has fallen. These observations have also suggested that the number of points of rain required in summer to stimulate the emergence of the adults depends on the penetration of rain into the soil and varies with the soil type.

Flight.

During the course of this study, beetles in the field flew only on particular nights in January, February and March. Usually beetles flew only on some nights

following peak periods of emergence from the soil. For convenience, a 'flight' will be said to have taken place when beetles have been observed or have been reported flying on one particular night; and the period of time after emergence when beetles may fly if weather is suitable has been designated a 'flight period'.

Flights of beetles at Mt. Gambier were recorded by observing beetles in flight before dusk and at dawn, by a mercury-vapour light-trap and by observations of beetles flying to and accumulating under mercury-vapour and incandescent street lights. A continuous record of flights was not made and many minor flights must have been missed. The flights which were recorded, however, mark the main flight periods, which are usually clearly demarcated and follow the emergence of large numbers of beetles from their cells after rain (fig. 2, a-c).

The beetles which emerged from the watered plots mentioned earlier, and beetles which emerged after rain on a number of occasions in the field, either flew away or crawled about on the surface of the soil on the first and subsequent nights they appeared above the soil. This difference in behaviour was related to the weather. If weather was suitable for flight, the beetles started flying about 15 minutes after sunset.

Temperature and wind velocity were the only two components of weather which had a noticeable effect on the occurrence of flight. Since Carne (1956) found a high correlation between sunset time and the initiation of flight each day, the wind speed and air temperature at 15 minutes after sunset at Mt. Gambier have been plotted for each day for the summers of 1954-56 to demonstrate their effect on the occurrence of flight after rain had stimulated the emergence of the beetles (fig. 2, a-c). Records of wind velocity were only available for 40 ft. above the ground; a wind velocity of about 10 m.p.h. at this height corresponds to a wind velocity of about 5 m.p.h. at ground level.

On nights when beetles flew, the air temperature was above about 58°F. and the wind velocity at ground level was below about 5 m.p.h., and on these nights the beetles ceased flying when the air temperature dropped below about 58°F. and the wind velocity exceeded about 5 m.p.h. These threshold values for flight may vary, however, with acclimatisation, with the physiological state of the insects and with interaction; there was, for example, a tendency for beetles to fly with a higher wind velocity if the air temperature was high.

The weather on the nights when the beetles were present but did not fly are also of interest, and if on any of these nights the beetles were known or expected to be in a physiological state in which they would fly but did *not* fly, it is *deduced* that weather was unsuitable for flight. On such nights the temperature was usually below 58°F. or the wind velocity at ground level above 5 m.p.h.

Physiological age of the female.

The beetles may live for 2-3 weeks after first emerging from the soil. They are crepuscular and are visibly active only after dusk. During the day they stay in the soil, in dung-pads or under objects on the surface of the soil. Much of their activity is not readily observable but may be deduced from the physiological age of the female, which was arbitrarily demarcated for different stages of the female's cycle of activity by observations on the development of the ovaries and the fat-body, and the presence or absence of food residues in the alimentary canal.

The gonads of the male are probably mature when the insect emerges from its cell, but there is considerable variation in the stage of development of the ovaries (fig. 3) during the female's cycle of activity. Usually a female lays one batch of eggs (about 35) without feeding and, if it survives, a second smaller batch (about 20) after feeding on dung.

Immediately after metamorphosis, the ovaries are immature (fig. 3, a) and the female lays eggs 10-14 days later if kept in moist soil; about a day before

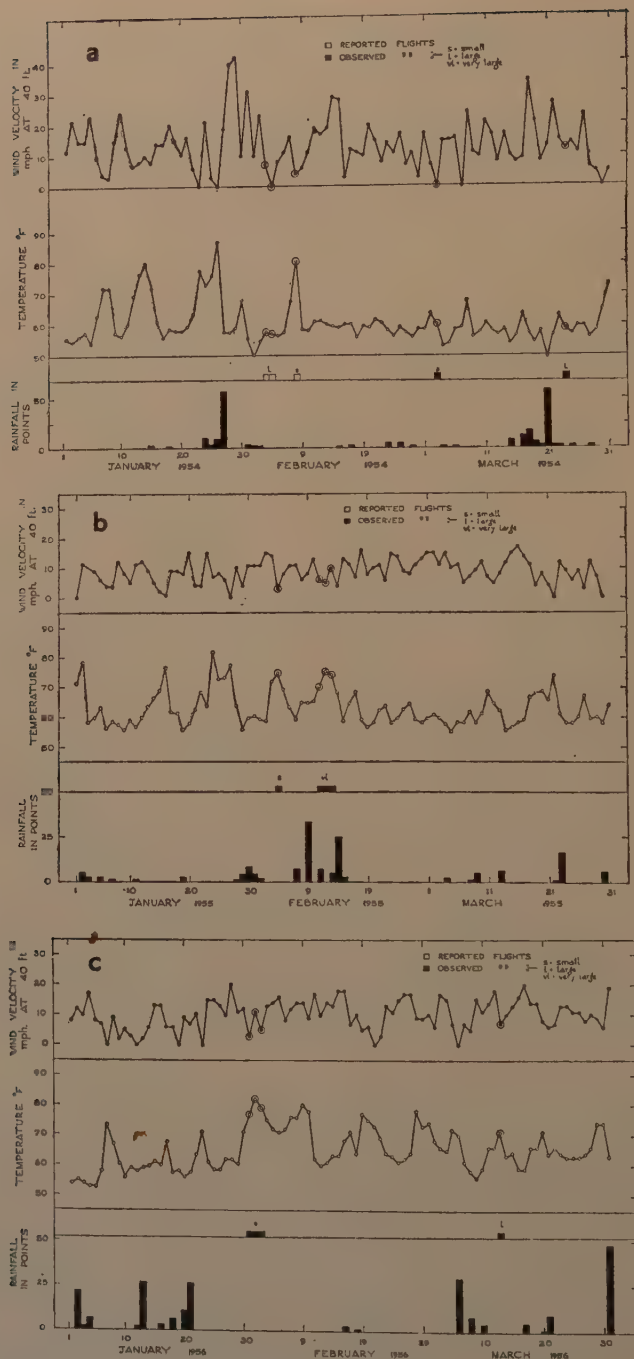


Fig. 2 (a-c).—The occurrence of flights of *A. tasmaniae* at Mt. Gambier in 1954–1956 in relation to rainfall and in relation to the weather at the expected time of initiation of flight each day during the flight season. For convenience, the wind velocity and temperatures on days when flights occurred are marked by circles. See text for further explanation.

oviposition the ovaries approximate to the stage c shown in fig. 3. Females collected in the field before emerging from their cells rarely have ovaries developed beyond stage b of fig. 3. After the females emerge, the ovaries develop rapidly and females kept in the laboratory laid eggs 3-6 days later. After the first batch of eggs has been laid, the ovaries appear again as in fig. 3, a. The female does not require to feed on dung to lay the first batch of eggs, but when weather is not

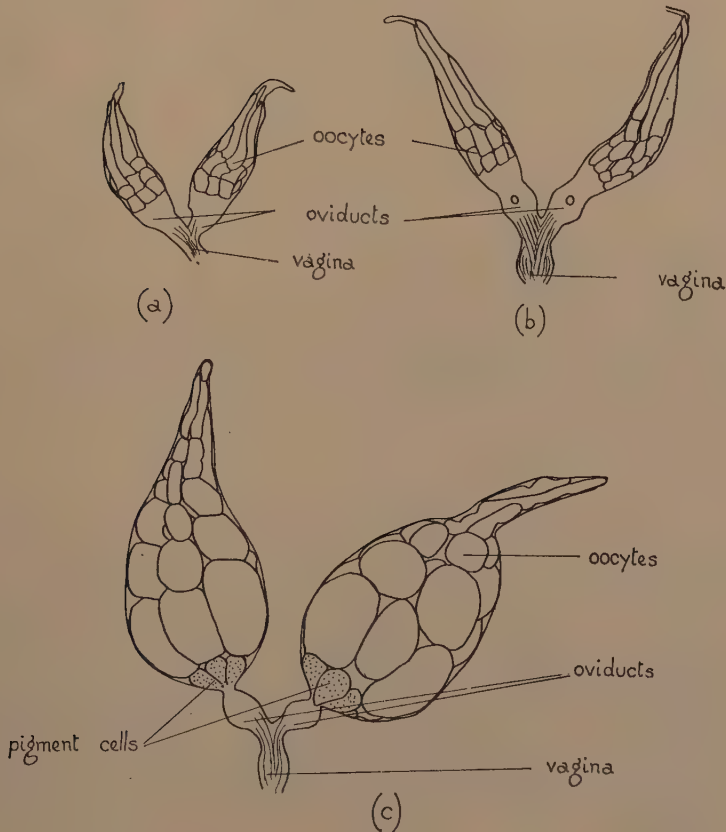


Fig. 3.—Stages in the development of the ovary of *A. tasmaniae* ($\times 32$). See text for explanation.

suitable for flight and the beetles crawl on the surface of the soil some of them may find dung and feed on it. However, even if the female does feed on dung before laying its first batch of eggs, the eggs are developed at the expense of the fat-body, and whether or not the first batch of eggs has been laid can be determined by the degree of depletion of the fat-body. The degree of depletion of the fat-body is also a useful criterion for demarcating the physiological age of the female during other stages of the female's cycle of activity (Table I).

TABLE I.

The determination of the physiological ages of females by various criteria.

Criteria	Stages in the cycle of activity of females					
	At metamorphosis	At emergence	Just before primary oviposition	Just after primary oviposition	Before secondary oviposition	After secondary oviposition
Ovaries in stage ..	a	b	c	a	b-c	a
Fat-body	++++	+++	++	+	—	—
Dung in alimentary canal ..	—	—	±	±	+	+

+ present
— absent

The effect of weather on primary oviposition.

In Table II are recorded, for each major flight, the number of days between the date of flight and the date on which rain fell and the physiological age of females participating in the flight. The flights fall into two natural groups, those which occurred 2-4 days after rain and contained females which had not laid their first batches of eggs, and those which occurred 7-12 days after rain

TABLE II.

The physiological ages of females participating in major flights, 1954-56.

Date of flight	Day on which rain fell and stimulated emergence from soil	No. of days between rain and flight	Condition of criteria for determining physiological age of females			Inferred physiological age of females before (B) or after (A) primary oviposition
			Ovaries	Fat-body	Dung in alimentary canal	
1954						
Mar. 3	Feb. 25	8	a	+	—	A
Mar. 24	Mar. 21	3	b-c	++	—	B
1955						
Feb. 4	Jan. 31	4	c	++	—	B
Feb. 11	Feb. 9	2	b	+++	—	B
Feb. 12	Feb. 9	3	b-c	++	—	B
Feb. 13	Feb. 9	4	c	++	—	B
1956						
Jan. 31	Jan. 21	10	a	+	—	A
Feb. 1	Jan. 21	11	a	+	—	A
Feb. 2	Jan. 21	12	a	+	—	A
Mar. 13	Mar. 6	7	a	+	—	A

+ present
— absent

and contained females which *had* laid their first batches of eggs. Since it is known that beetles will fly on the first day they emerge from the soil if weather is suitable, it follows that, when the beetles flew 2-4 days after rain, weather was suitable for flight when they first emerged from the soil, and, when beetles flew 7-12 days after rain, weather was not suitable for flight when they first emerged from the soil. If the data in fig. 2 are examined it can be seen that these deductions can be verified on some occasions. For example, following rain on 21st January 1956, beetles emerged on the 24th January 1956, but the wind velocity on this evening and again on that of 25th and 26th January was well above the threshold value and the beetles did not fly.

Similarly, 30 points of rain fell at Mt. Gambier on 6th March 1956, and beetles first emerged from the soil at dusk on 9th March. Wind velocity and temperature were unsuitable for flight on 9th March, and large numbers of beetles crawled about on the surface of the soil. Similarly, on 10th March and 11th March, wind velocity at least was unsuitable for flight, and beetles were observed crawling on the surface of the soil but in decreasing numbers. Until 11th March none of the females picked up from the surface of the soil had laid any eggs. On 12th March, wind velocity was again unsuitable for flight and very few beetles were crawling on the surface of the soil; some of these, however, had laid their first batches of eggs. Then, on 13th March, wind velocity was low and temperature was high, and large numbers of beetles were observed flying; as recorded in Table II, the females flying on this night had all laid their first batch of eggs. The above observations also suggest that the beetles in the field, as in the laboratory, lay their eggs 3-6 days after emerging from the soil. The decreasing numbers of beetles on the surface of the soil on 9th, 10th, 11th and 12th March suggest that the females, at least, becoming gravid, had stayed in the soil whilst in this physiological state. Similarly, in 1955, flights occurred on 11th, 12th and 13th February, commencing with very large numbers on the 11th and decreasing to only a few on the 13th. On 14th February, although weather was obviously suitable for flight, virtually no beetles were flying or were on the surface of the soil. Beetles in samples taken on 11th February started laying eggs on 15th February, and the mortality-rate of the beetles was low until about 20th February. The decrease in the numbers of beetles flying in the field over the period 11th-14th February was probably partly due, therefore, to the females becoming gravid and staying in the soil; the males were probably flying to dung.

If the above deductions are correct they mean that 2-3 days after emergence, the beetles enter a physiological state in which they are not stimulated to fly or are not stimulated to fly to lights. It is not known how the physiological status of the beetles influences the occurrence of flights later on in the cycle of activity, so at present the suitability of weather for flight can only be inferred for the first two or three days after the beetles emerge or for days when flights have been observed to occur.

The relation between flight and the physiological age of females.

Beetles flying in South Australia before dark and at dawn have been observed flying at random only if it was calm or else flying with the wind, and it was shown by the use of cloth screens around light-traps that beetles flying to light-traps after dark also flew downwind if there was any wind. Samples have indicated that the females caught in light-traps had ovaries in one of the stages, (a), (b) or (c) shown in fig. 3, that they all had some fat-body and none had fed on dung (Table II). Beetles netted in flight also had ovaries in any one of the three stages, all contained some fat-body and the majority had not fed on dung. An occasional female netted in flight before dark or at dawn *had* fed on dung, but since these beetles also flew with the wind, if there was any wind, and so were

clearly *not* flying to dung-pads, it is suggested that they had found dung and fed on it whilst crawling on the surface of the soil. Similarly, adults of the closely allied species, *Aphodius pseudotasmaniae* Given, have been observed flying downwind in Tasmania; the females either had immature ovaries or some mature eggs (Martyn, 1950). However, Carne (1956), in Canberra, only observed swarms of adults of *A. tasmaniae* flying upwind to dung-pads. Such flights have not been observed in South Australia. However, in cattle pastures, large numbers of beetles in dung-pads have sometimes been observed, and have only been observed after the weather has been suitable for flight at least once since the mass emergence of beetles from the soil; it may be inferred, therefore, that when large numbers of beetles occur in dung-pads they get there by flying. It has further been observed that dung-pads which swarm with beetles may often be found only a few feet from seemingly identical dung-pads which are devoid of beetles. Such aggregations of beetles in particular dung-pads are not at variance with, and are most plausibly explained by, upwind flights to dung similar to those documented by Carne.

The females found in dung-pads usually had no fat-body or virtually no fat-body and had laid their first batches of eggs. The females which fly to dung in South Australia are therefore those which usually have laid their first batches of eggs and have largely depleted their fat-bodies. On 2nd February 1956, for example, many hundreds of beetles were known to have been in dung-pads but the females caught at lights on this night had not fed on dung and had some fat-body (Table II). These observations suggest that some time after laying their first batches of eggs a physiological stimulus induces a behaviouristic change in the females, which then fly upwind to dung and are not attracted to lights; this physiological stimulus is probably related to the final depletion of the fat-body.

The behaviour of the adult feeding on dung has been discussed by Carne (1956), who records that "fully-fed" gravid females constitute the *bulk* of the female population attracted to lights. Such females have never been caught at light-traps in South Australia, but this may be because observations on the activity of beetles have usually been confined to a period of about 10 days after major peaks of emergence of beetles from the soil and fully fed, gravid females are probably not found until 12–15 days after rain.

However, if rain stimulates the emergence of beetles in Canberra, there is a contradiction in Carne's data. To become a fully fed, gravid female, a female has to lay its first batch of eggs and then fly to dung and feed on it until its second batch of eggs is mature. Fully fed, gravid females are probably not found, therefore, until 12–15 days after rain. Carne's light-trap data, however, indicate that large numbers of beetles were frequently caught 2–4 days after rain (see particularly Carne, fig. 2). His data suggest that adults of *A. tasmaniae* in Canberra emerge after rain and that, if weather is suitable for flight when they emerge from the soil, they fly to light-traps rather than to dung-pads. Such behaviour would be consistent with Martyn's (1950) observations on *A. pseudotasmaniae* in Tasmania and with my observations on *A. tasmaniae* in South Australia. It is probable therefore that the behaviour of adults of *A. tasmaniae* and of *A. pseudotasmaniae* can be summarised as follows:

Beetles first emerge from the soil 48–72 hours after rain. The females fly before laying any eggs if weather is favourable for flight within 2–3 days of the emergence of the beetles. If, however, weather is unfavourable for flight for 4–5 days after emergence the females lay their first eggs before flying. Until their fat-body is largely depleted, beetles fly with the wind and are attracted to lights, but, after this stage has been reached, they fly upwind to dung and are not attracted to lights. After feeding on dung for a few days the females become gravid, change their responses again to light and perhaps wind, and aggregate in certain places in which the second batches of eggs are laid

The effect of weather on the site of oviposition.

Summer rainfall in South Australia is deposited either by cold fronts or by tropical thunderstorms, and the type of weather which brings rain tends to persist for 5–6 days after the rain. Wind direction and temperature—and wind velocity, to a lesser extent—are functions of air mass types encountered in South Australia. When adults emerge after frontal rain, the wind is usually moving through south-west to south to south-east, the wind velocity is usually above 5 m.p.h. and the temperature is usually low; the adults usually, therefore, do not fly until the weather becomes warmer and the first batches of eggs are laid before the adults fly. These eggs are consequently laid near or in the places in which the larvae damaged pasture the previous year, and the recolonisation of the damaged areas results in the areas of damage being enlarged. When, however, the beetles emerge after thunderstorm rain, it is usually oppressively calm or a gentle wind is blowing from the north-east, north, or north-west and the temperature is high; the adults usually, therefore, fly as soon as they emerge, *i.e.*, before the first batches of eggs are laid. The eggs are then not laid near or in the places in which the larvae damaged the pasture the previous year but are laid in other places in which the adults aggregate. In 1955, for example, virtually only one flight occurred and this was after thunderstorm activity. In the winter of 1955, larvae of *A. tasmaniae* caused extensive damage to pastures, but very few larvae were found in areas which were damaged the previous year.

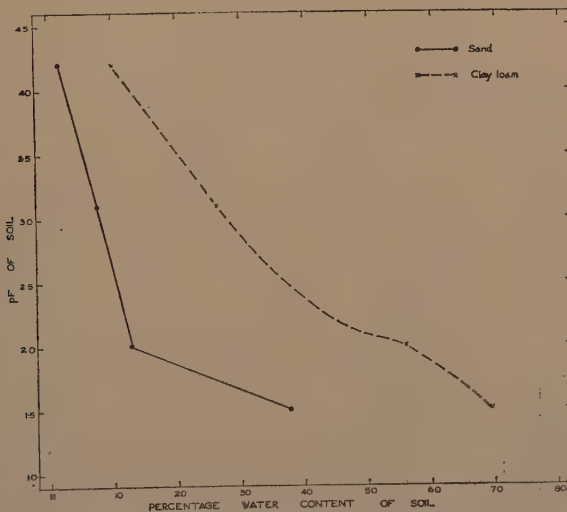


Fig. 4.—The pF/water-content curves for Wandilo sand and Mt. Schanck clay loam. As the loam was of disturbed structure the value at pF 2.0 for this soil would not be related to the field capacity *in situ*.

Since fewer females survive to lay a second batch of eggs and since the second batches of eggs are smaller than the first, the first batches of eggs probably contribute 70 per cent. or more to the total eggs laid. It is important, therefore, to determine the sorts of places in which the first batches of eggs are laid, particularly when the females fly before laying them. The factors which influence the aggregation of adults in the field have therefore been studied.

The effect of water in the soil on oviposition and on the survival-rate.

The water content of soil is known to affect markedly the birth-rate and death-rate of animals living in soil. Adults of *Lachnosterna* (*Phyllophaga*) sp., for example, laid most eggs and survived for the longest time in a particular range of water content of soil (Sweetman, 1931). The rate of loss of water from wireworms in soils of various water contents was shown, however, to be a function of the force with which the water was held (pF) rather than the water content of the soils (Evans, 1944). Similarly, the rate of production and size of cocoons of earthworms could be correlated with the pF values of soils rather than their water contents (Evans & Guild, 1948). Females of *A. tasmaniae* lay eggs in a variety of soils; experiments were therefore conducted with soils from two localities in the study area, namely a sand from Wandilo, and a clay loam from Mt. Schanck, to determine whether the beetles responded to the 'available' water in the soil. The experiments were conducted before the pF/water-content curves (fig. 4) for the two soils had been worked out; they were consequently conducted with water contents and expressed later as pF values.

A number of beetles which had not laid their first batches of eggs were caught at a light-trap on 4th March 1955. On the following day, 20 copulating pairs of beetles were placed in boxes of soil with various water contents; there were two replicates to each treatment. The boxes of clay loam were examined after nine days and the boxes of sand after nine and 14 days, and the numbers of eggs laid and the numbers of beetles alive at each water content were recorded.

The mean number of eggs laid per female are plotted against the percentage water contents of the two soils in fig. 5 and against the equivalent pF values in

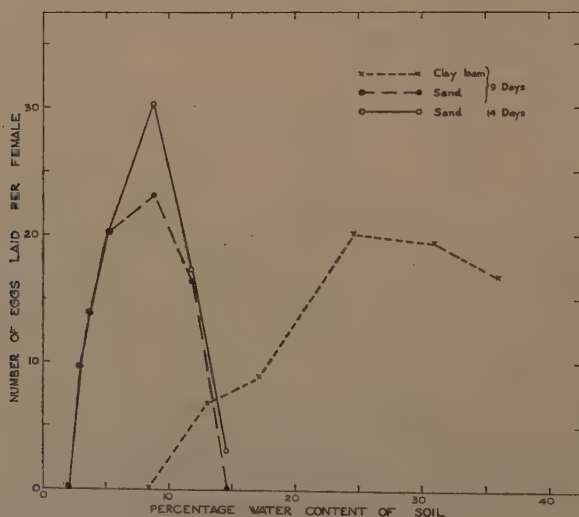


Fig. 5.—The number of eggs laid by females of *A. tasmaniae* in relation to the water content of two soils.

fig. 6. The closely corresponding curves for both soils when the water content of the soil is expressed on the pF scale suggest that the beetles responded to the force with which the water was held, i.e., the 'available' water in the soil. An analysis of variance indicated that the differences in the mean numbers of eggs

in a batch could be attributed to chance ($P > 0.20$); dissections of dead beetles showed that the larger number of eggs laid in the optimum range of moisture in soil was due to more beetles laying all their eggs rather than all the beetles laying more eggs.

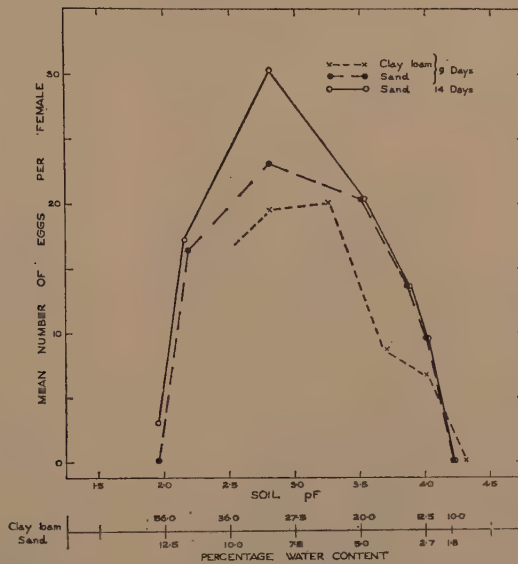


Fig. 6.—The number of eggs laid by females of *A. tasmaniae* in relation to the pF value of two soils. The water contents of the two soils over the range of pF are added for reference.

The percentage mortality of beetles is plotted against the water contents of the soils in fig. 7, and the percentage mortality of females after nine days is

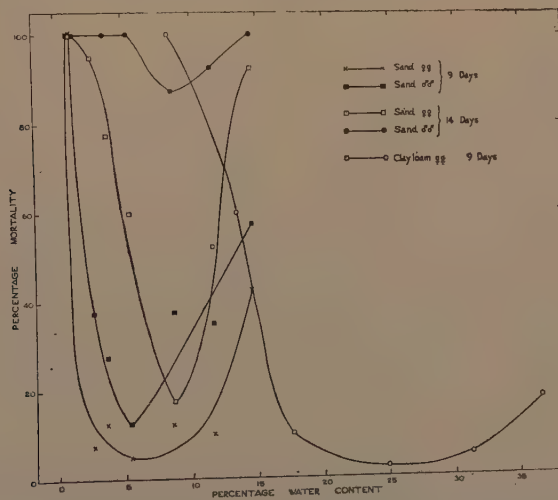


Fig. 7.—The mortality of adults of *A. tasmaniae* in relation to the water content of two soils.

plotted against the pF values of the soils in fig. 8. The mortality curves have been drawn by eye, but the striking resemblance of the mortality data in the two soils, when plotted against the pF values of the soils, indicates that the death-rate was determined by the available water in the two soils. It is interesting to notice that the range of pF which was optimal for survival (*i.e.*, 2.8–3.2) was also the range in which most eggs were laid.

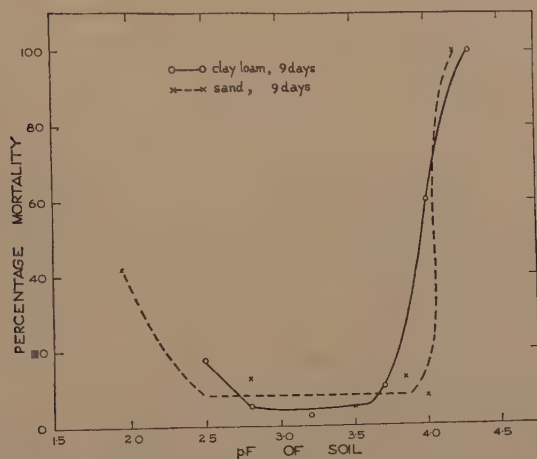


Fig. 8.—The mortality of females of *A. tasmaniae* after nine days in relation to the pF value of two soils.

Some of the experiments described below were conducted to determine whether beetles would aggregate in the range of pF 2.8–3.2 if given a choice between levels of moisture in soil.

Factors influencing the aggregation of beetles.

Larvae of *A. tasmaniae* are found mainly in pastures which had a very thin cover of stubble (dry herbage) or no cover in late summer (Pl. XVII, figs. 1, 2). H. G. Andrewartha (private communication) suggested that the bareness of these pasture surfaces was a "token" stimulus and that beetles aggregated in these pastures in relation to the water content of soil, which is usually higher under a bare surface than under a cover of stubble (Table III).

Swan (1934), on the other hand, suggested that the beetles were attracted to the accumulation of dung so often present in the areas in which the eggs are apparently laid, and Carne (1956) suggested that (1) paddocks containing newly germinated clover were attractive to beetles and that the clover facilitated burrowing (2) adults in flight were attracted to other adults in the soil.

The following experiments were conducted to determine which of the factors mentioned above influenced the choice by females of places in which to lay eggs.

Laboratory experiments.

The apparatus used in these experiments was a simple 'choice' chamber. The lower half of a wooden box, 1 ft. square and 1 ft. deep, was divided into quarters by means of a waterproofing paper. Soil was placed in each quarter and was tamped down so that its surface was only three- or four-sixteenths of an inch

above the dividing partitions. Then the top tenth of an inch or so of soil was loosened lightly with a needle, to facilitate burrowing by the beetles, except where a compact surface was a treatment in any experiment. The beetles consequently were not able to burrow from quarter to quarter through the soil but were obliged to enter any quarter of soil from the surface. The effective soil depth was 6 in.

Beetles were always introduced into the boxes at dusk so that their behaviour would be disturbed as little as possible, and a quarter of the number used in any experiment was placed on the surface of each quarter of the box. At the termination of an experiment the soil was dug up from each quarter of the box and the number of live beetles and eggs was recorded.

All the beetles used in these experiments, except those used in experiment VII, were caught in a light-trap on 11th February 1955, on the first day they emerged from the soil and before the females had laid their first batches of eggs. The beetles were kept in a box of moist soil until required and came to the surface each night and crawled about and mated. After the first night it is probable that all the females had mated, so in some experiments only females were used. There were usually two replicates (two boxes) in each experiment.

In the first series of experiments beetles were given a 'choice' of four water contents of soil. In later experiments the water content of the soil was kept constant and the beetles were given a choice of various sorts of surfaces.

(a) *The effect of water in the soil (experiments I, II, III).*—The details of the experiments were as follows:—

Expt. no.	Beetles given a choice of pF values	Type of soil	No. of beetles used	Duration of expt. (days)	No. of replicates
I	4.0, 3.5, 2.8, 2.15	sand	200 ♀♀	2	2
II	4.2, 3.85, 3.5, 2.8	sand	200 ♀♀	3	2
III	3.7, 3.2, 2.8, 2.5	clay loam	200 ♀♀	3	2

The results of these experiments are given in Table IV. Those of experiment I indicate that females aggregated in the range of pF 2.8–3.5 before laying eggs; the response to water in soil is probably related therefore to the survival of the beetles and is not a specific response for oviposition. When experiments II and III were conducted the females were older and had more mature ovaries. The results indicate that:—

- (1) the beetles aggregated at pF 2.8 in the sand in experiment II, and aggregated within the range of pF 2.8–3.2 in the clay loam in experiment III,
- (2) the number of egg-batches laid in each moisture level of soil was roughly proportional to the number of beetles aggregated there.

It has been mentioned that the experiments were conducted before the pF/water-content curves had been worked out, and it is unfortunate that the beetles in these three experiments were not given a choice of the same pF values in both soils. In the sand (experiments I and II), pF 2.8 was clearly the optimum of the pF values used; this was also the pF value in sand at which the beetles lived for the longest time and the females laid most eggs. It is probable that the clarity with which pF 2.8 stood out as the optimum in the sand was due to the spacing of the moisture levels tested. The response to water in soil is likely, however, to be normally distributed, and a further series of tests with a larger number of pF values at close intervals would probably reveal, not a single optimum water content, but a range of optimum water content.

The results of the experiments with clay loam are instructive, therefore, because the water contents which were used were spaced closer together than those of the sand. A single optimum water content could not be clearly distinguished in the clay loam, and the results indicated rather that there was an optimum range of pF 2.8-3.2 in which the adults aggregated, lived the longest and laid the most eggs.

The combined data are only intelligible if the response of the adult is related to the pF value of the soil, and indicate that there is an optimum range of "available" water for the beetles in both soils, probably within the vicinity of pF 2.8-3.2. The pF scale thus provides a convenient basis for comparing the behaviour of the beetles over a range of water contents in two soils, and for assessing the effect of moisture in soil on the death-rate and fecundity of the adults.

It is tempting to speculate on the physiological basis for the reaction of the adults to the pF value of soil rather than its water content. Larvae of *Agriotes* sp. similarly migrate rapidly out of dry soils and aggregate in wet soils; this behaviour has been ascribed to the differential effect of moisture on the rate of burrowing, the intake of water by the insects in wet soil resulting in akinesis (Lees, 1943). A 0.33M sucrose solution was approximately isotonic for larvae of *Agriotes* sp. and, in hypotonic solutions, the wireworms were constantly imbibing, through the cuticle, water which was subsequently excreted (Evans, 1944). Since a 0.33M solution of sucrose has a pF value of 3.94, wireworms are expected to imbibe water in soils which are wetter than pF 3.94, and the amount which they imbibe will probably be related to the pF value of the soil. It is probable therefore that if they were given a choice of soils they would aggregate in relation to the pF values of soils rather than their water contents.

There is no evidence that the aggregation of adults of *A. tasmaniae* in moist soil is a result of akinesis brought about by imbibing water through the cuticle. Instead, the beetles appear to react rapidly to moisture on the surface of the soil or in the top half-inch of soil (see also experiment VI, below) and will not attempt to burrow in soil which is very dry (pF 4.0) or very wet (pF 2.0). In soil which is wetter than pF 2.8 they might react to excess water or to a lack of oxygen. The pore-space distributions of the two soils used in the experiments are different, but the beetles appeared to behave similarly in both soils when the soils were wetter than pF 2.8, so it is probable that they responded to excess water. If this is true, adults of *A. tasmaniae* must have receptors which respond to 'available water' in soil.

(b) *The effect of shelter (experiment IV).*—*A. tasmaniae*, as has been mentioned, often lays large numbers of eggs in areas where there is an accumulation of dung, e.g., sheep 'camps'* (Pl. XVII, fig. 3), but the beetles readily burrow under any object on the surface of the soil and often lay eggs under straw (dry grass stems broken off the parent plant), boxes, bales of hay, logs, etc., lying on the surface. An experiment was therefore designed to determine whether adults were attracted to dung or whether accumulations of dung acted as 'shelter'.

The surfaces of soil in the choice chamber were:—

- (1) bare but with scattered particles of dry dung fragments to act as attractant.
 - (2) bare.
 - (3) a layer of straw as shelter.
 - (4) a thick layer of dry dung fragments as found in sheep camps to act as shelter.
- The pF value of the soil in the boxes was 2.8; one hundred beetles of each sex were used in each of two replicates.

* Places where sheep habitually congregate to rest.

The results are given in Table V. No significant difference was found between the sexes in the different treatments, so the numbers of each sex were used as further replicates in each box. The analysis of variance indicated that the numbers of beetles found under the different surfaces differed significantly ($P < 0.001$). The difference between 'bare' surfaces on the one hand and surfaces with shelter on the other was highly significant ($P < 0.001$); the differences between the two types of shelter, and between the two types of 'bare' surface, were not significant. Dry dung thus had no value as an attractant, but the data suggested that it could promote the aggregation of adults by acting as 'shelter' if it was in sufficient quantity.

TABLE V.

The attraction of shelter to adults; the numbers of beetles recovered from different treatments in experiment IV.

Treatment no.	Treatment	Number of beetles in replicate				Total	Mean
		1		2			
		Male	Female	Male	Female		
1	Bare soil with dung as attractant	19	21	22	16	78	19.5
2	Bare soil	12	20	15	13	60	15.0
3	Shelter, straw	36	27	37	42	142	35.5
4	Shelter, dung	33	32	22	30	117	29.3

Analysis of variance between	Difference between means	Minimum difference for significance at $P=$		
		0.05	0.01	0.001
Any two treatment means	see above	7.90	11.97	19.25
Bare soil and soil with shelter ..	15.15	4.90	6.80	9.46

(c) *The effect of type of surface (experiment V).*—The following experiment was conducted to determine whether adults would aggregate in areas whose surfaces were loose and which could be penetrated rapidly.

The boxes were filled with soil of pF 2.8 and the surfaces were as follows:—

- (1) top half-inch of soil loosened.
- (2) loosened by the burrowing of beetles (50 females were placed on the surface and the beetles allowed to burrow into the soil before the experiment began).
- (3) bare and compact.
- (4) bare and compact with 20 dead females on the surface to act as a possible attractant.

At dusk, 50 females were placed on the surfaces of treatments 1, 3 and 4 so that 200 were used altogether. The numbers of beetles which were recorded in the different treatments 3 days later are tabulated in Table VI.

It was not possible to decide how many beetles were attracted to the loose soil on the surface of treatment 2 and how many were attracted to the beetles

in the soil, because the original 50 which burrowed into the soil probably came to the surface and dispersed and the number of new arrivals could not therefore be estimated. It is clear, however, that the numbers of beetles under surfaces 1 and 2 were similar and differed significantly from the numbers of beetles under surfaces 3 and 4, which were also similar. A loose surface therefore favours aggregations of adults. Germinating clover could, therefore, as Carne (1956) suggests, promote aggregations of adults by providing innumerable points of entry into the soil; but germinating clover is probably not an important factor in South Australia because the rain which stimulates the clover to germinate also stimulates the emergence of the beetles, and the beetles usually have emerged before the clover breaks the surface of the soil.

The data above also indicate that adults aggregated where other beetles had previously burrowed and did not aggregate where there were dead beetles on the surface. This subject is discussed further below.

(d) *The relative influence of water and shelter (experiment VI).*—In this experiment the surfaces were:—

- (1) Scattered particles of fresh dung as an attractant on dry soil—loose surface.
- (2) Shelter on dry soil—loose surface.
- (3) Shelter on wet soil—compact surface.
- (4) Bare wet soil—compact surface.

Two hundred females were used in each of two replicates. The soil was Wandilo sand.

The dry soil had a pF value of 4.2, and, being dry, could not be compacted and necessarily had a loose surface; the wet soil had a pF value of 2.8. The shelter used in both treatments 2 and 3 was a half-inch layer of dung plus straw débris. The numbers of beetles recorded under the different surfaces after three days are given in Table VII. The outstanding feature of this experiment was the aggregation of *all* the living beetles in the wet soil despite the attractiveness in other circumstances of shelter, loose surface and fresh dung on the dry soil surfaces. The other interesting feature of the experiment was that there were more beetles ($P < 0.001$) under the bare, wet, compact surface than under the wet, compact surface with shelter, despite the previously demonstrated attractiveness of shelter. This was probably because the half-inch layer of shelter was relatively dry compared with the top half-inch of the bare, wet, compact surface.

The data demonstrate the outstanding importance, for aggregation, of water in soil and suggest that the moisture content of the top half-inch of the soil surface is important in promoting or inhibiting aggregations of adults.

(e) *The effect of other individuals of A. tasmaniae (experiment VII).*—Discontinuities in the distribution of larvae of *A. tasmaniae* in pastures may be related to obvious factors such as soil moisture, obstacles, pasture type, etc., but sometimes the larvae occur in restricted areas in pastures which "appear to be uniform" (Carne, 1956). Their patchy distribution in such pastures may be the result of more eggs being laid or more eggs or larvae surviving in certain places.

If more eggs are laid in certain places there must be aggregations of adults in these places. To explain the necessary aggregations of adults, Carne (1956) suggested that females may possess some olfactory or auditory mechanism whereby they can detect the presence of other females, or possibly larvae, in the soil. An experiment was therefore conducted to determine whether females were attracted to other adults in the soil.

The data of experiment V suggested that adults aggregated in places where other adults were, or had been, in the soil. The following experiment was designed to enable separate estimates to be made of the relative attractiveness of loose soil at the surface and of adults in the soil; it relies on the assumption that, if it

were shown that adults crawling on the surface are attracted to others burrowing in the soil, then adults in flight might be attracted to others burrowing in the soil.

Twenty beetles were enclosed in a 1 ft. \times 1 ft. \times 1 ft. wire-mesh cage a half-inch under some of the soil surfaces, and some of the surfaces were loosened artificially, others were compacted. The treatments were as follows:—

- (1) Compact surface—beetles under the surface.
- (2) Loose surface—beetles under the surface.
- (3) Compact surface—no beetles.
- (4) Loose surface—no beetles.

The beetles used in this experiment were caught at a light-trap on 1st February 1956. The females had laid their first batches of eggs; so the beetles were kept in moist soil and fed on dung for four days before the experiment. One hundred beetles of each sex were used in each of four replicates; the soil was Wandilo sand of pF 2.8.

The numbers of live beetles under the different surfaces were recorded two days later. Different numbers of males and females died in the course of the experiment, so the numbers of each sex were corrected to the numbers expected if all the beetles had survived; these are tabulated in Table VIII. The inclusion of sex in the analysis increased the number of 'treatments' to eight. The analysis of variance revealed that the differences between the treatments were highly significant ($P < 0.001$). The treatment sum of squares was divided into (a) a component for sex which was zero because the same number of males as females was used in the experiment, (b) a component for the four types of surface, and (c) a component for the interaction of sex and types of surface, which can be attributed to the differences in distribution of the two sexes. The variance ratios of the components indicated that the differences between the types of surface were highly significant ($P < 0.001$), and that the difference in the distribution of the sexes in the types of surface could be attributed to chance ($P > 0.05$). Partitioning the sum of squares for types of surface into its components indicated that (1) beetles were not attracted to other beetles under the surface ($P > 0.05$), (2) aggregations of adults occurred wherever the surface soil was loose ($P < 0.001$).

The results of experiment V also indicate that beetles aggregated in areas in which the surface soil was loose. The magnitude of the differences between loose and compact surfaces in both the experiments provides convincing evidence that beetles will aggregate on surfaces which can be penetrated readily, and suggests that, in experiment V, the adults aggregated in the areas in which other beetles had burrowed because the original beetles had made the surface soil more favourable for burrowing.

The results of experiment V also suggested that beetles were not attracted to dead beetles on a compact surface. Adults may possibly aggregate, however, in areas where there are dead adults on a loose surface rather than a compact surface because compact surfaces ordinarily inhibit aggregations of adults (experiment V). This possibility was not tested but, in view of the effect of the loose surface itself on the aggregation of adults and the observation that in the field the adults usually die in the soil rather than on the surface, it is improbable that there exists an attraction *per se* of adults to dead adults of a magnitude necessary to explain aggregations in apparently uniform pastures.

The only type of attraction left to be considered is that of adults to other live adults on the surface of the soil. In the laboratory, when temperatures were high and adults were extremely active, the adults on the surface of the soil sometimes came together to form a loose aggregation* which developed into a

* In the sense used here aggregation means a dynamic, co-ordinated system, the parts of which are related to and affect the other parts and, perhaps, the system as a whole. In all other contexts aggregations=accumulations, with no implication of a direct effect of one beetle on other beetles.

tight group of beetles milling around an individual which had started to burrow, and then all the beetles disappeared into the soil down the same hole. When temperatures have been high, similar tight groups of milling adults have been observed in the field in places in which a number of individuals have accumulated on the surface of the soil, *e.g.*, under lights; and Carne has observed loose aggregations of adults before flight. Such aggregations are probably formed by mutual stimulation of adults already on the surface, but their occurrence is probably rare except in places where adults accumulate by chance, *e.g.*, along the edges of infested areas following the emergence of beetles from their cells, and under trees after flight (see below). There is no evidence that beetles which are flying are attracted to such loose aggregations on the surface of the soil. Nor indeed is this hypothesis necessary to explain the aggregations of larvae even in seemingly uniform pastures because, even in such pastures, considerable variations in the water content of the soil may occur within feet and may profoundly affect the distribution of eggs (see below).

Field experiments.

Two experiments were conducted, on the clay loam (*terra rossa*) soils of Mt. Schanck, to determine whether beetles would aggregate in the field in response to certain stimuli as they did in the laboratory. In each experiment a block, consisting of plots with various types of surface, was surrounded by strips of metal placed in the soil and was covered with wire gauze after beetles were placed on the surface of the soil on 16th February 1955. The types of surfaces were replicated twice.

Originally it was intended to dig up the soil 3-4 days later and record the number of eggs which had been laid and the number of beetles which had aggregated under the different types of surfaces. Because another experiment could not be done, however, the eggs laid and the larvae which hatched from them in the plots had to be used to estimate the effect of drought on the survival-rate of young larvae. The blocks were consequently covered uniformly with a layer of dung and organic matter 14 days after the experiment began and replicates were dug up at various times to estimate the survival-rate of young larvae.

It was expected from the data of experiments II and III that the number of eggs or young larvae found in the positions corresponding to the original types of surface would be proportional to, and hence could be used to estimate, the number of adults which had aggregated under the different types of surface. But many dead beetles were also found when the plots were dug up, and the ratios of larvae to dead adults were so similar for the various plots that either the numbers of dead adults or of larvae can be used with confidence to estimate the proportion of adults which aggregated under the types of surface with which they were present.

The details of the experiments were as follows:—

(a) *The effect of shelter and type of surface (experiment VIII).*—An area was specially chosen so that the surface of the soil in some of the plots would be compact and difficult to penetrate. It was located near a gate where the trampling of cattle had removed the pasture coverage and had compacted the soil within a radius of 10 ft. or so from the gate. Beyond this radius, pasture was growing normally; at this time of the year it consisted of a few plants of perennial rye-grass with a smattering of stubble and loose straw on the surface.

TABLE IX.

The effect of shelter and type of surface; the numbers of adults and larvae recovered from different treatments in experiment VIII.

Treatment no.	Treatment	Plot 1			Plot 2			Total		
		Adults	Larvae	Larvae/ adults	Adults	Larvae	Larvae/ adults	Adults	Larvae	Larvae/ adults
1	Bare compact ground	12	73	6.08	4	13	3.25	16	86	5.4
2	Bare compact ground with shelter	124	731	5.90	136	889	6.54	260	1620	6.2
3	Pasture	89	547	6.15	95	602	6.34	184	1149	6.4
								Total 460	2855; \bar{x} = 6.2	

Comparing treatments 2 and 3; $\chi^2 = 13.1$, $P < 0.001$.

It was not possible to randomise the types of surfaces, so the plots, each 2 ft. square, were arranged within the experimental block as follows:—

Pasture (replicate 1)	Bare, compact ground covered with shelter (replicate 1)	Bare, compact ground without shelter (replicate 2)
Pasture (replicate 2)	Bare, compact ground without shelter (replicate 1)	Bare, compact ground covered with shelter (replicate 2)

The shelter was a half-inch layer of straw and dung from a sheep camp and was placed on the bare, compact surfaces where stipulated. One hundred females were placed on each plot. The results are given in Table IX.

A test of homogeneity, using the numbers of dead beetles, suggests that there were significantly greater numbers of adults in the soil under shelter than under pasture ($P > 0.001$), but the non-randomised positions of the sub-plots might account for the difference. The difference between bare, compact ground with and without shelter is not affected so much by the experimental design, and the magnitude of the difference demonstrates how unattractive was the bare ground without shelter. In fact, the few beetles and larvae which were found in the sub-plots without shelter were found along the strips of metal where the soil was probably not so compact. The data generally agree with the laboratory data and indicate that (1) the readiness with which adults can burrow into the surface of a soil is an important factor in promoting aggregations of adults. (2) the top half-inch of the soil surface is all-important in promoting or inhibiting aggregations of adults; half an inch of shelter can transform an unattractive surface into one under which beetles will aggregate readily and lay eggs.

(b) *The necessity of water for oviposition (experiment IX).*—This experiment was designed initially to test the relative attractiveness of shelter and a loose surface to adults. There were two replicated plots, each 3 ft. square, and each replicate was divided into four squares which had the following surfaces:—

- (1) Bare ground—soil loosened at surface.
- (2) Bare but with small pieces of dry dung as attractant.
- (3) Bare ground—layer of dry dung as shelter.
- (4) Bare ground—cover of straw as shelter.

Fifty females were placed on each sub-plot.

TABLE X.

The necessity of moisture for oviposition; the numbers of adults and larvae recorded from different treatments in experiment IX.

Treatment	Plot 1			Plot 2*			Total adults
	Adults	Larvae	Larvae/ adults	Adults	Larvae	Larvae/ adults	
Bare, loose surface	62	757	12.1	11	49	4.1	73
As above with dung as attractant	38	548	14.2	70	262	3.7	108
Layer of dung as shelter	63	720	11.4	53	157	3.0	116
Layer of straw as shelter	14	159	11.4	51	270	5.3	65
Total	177	2184		185	738		362

* Note: Plots 1 and 2 were dug up at different times.

The results are given in Table X. The numbers of adults and larvae found under different replicates of the same surfaces differed considerably, suggesting that none of the surfaces influenced the aggregation of the adults. There was evidence, instead, that moisture was a limiting factor and that the erratic distribution of the insects was due to the erratic distribution of pockets of soil with a favourable water content for survival and egg-laying. It was noticed, whilst digging up the sub-plots of replicate 1, that particular patches of soil were wetter than others and that most of the first-instar larvae occurred in aggregations in these particular patches. The young larvae were still in the cells in which the eggs were laid, so more eggs had either been laid or had survived in the wetter patches of soil; and since most of the beetles were found in the wet patches the relative scarcity of larvae outside the wetter areas was probably due to fewer eggs being laid rather than fewer eggs surviving.

The data indicate the variability in the water content of the soil which may occur within a small area in a seemingly uniform pasture, and the profound effect of this variability on the distribution of eggs of *A. tasmaniae*. They clearly indicate the importance of moisture in soil for oviposition and suggest that in the summer of 1955 the 66 points of rain which stimulated the emergence of beetles were not sufficient to make extensive areas favourable for oviposition on the clay-loam soils of Mt. Schanck.

Discussion.

It is difficult to determine the distribution of eggs of *A. tasmaniae* in the field, so the kinds of places in which females lay eggs have been inferred by observing the kinds of places in which the larvae have occurred and by determining the characteristics which the infested areas had in common at the time of flight. This method neglects places in which eggs are laid and do not survive, but such places are probably few because the eggs develop rapidly and the adults tend to lay eggs in a range of water in soil well within the range required by the egg for normal development. The inferences drawn in this way about aggregations of adults are supported by the readiness with which the adults responded to certain stimuli in the laboratory and indicate that aggregations of adults in the field are brought about by the responses of the adults to moisture in soil, type of surface and shelter.

The most obvious visible characteristic of pastures damaged by larvae of *A. tasmaniae* is the relatively bare surface in summer (Pl. XVII, fig. 2); few larvae occur in places which were covered by dense stands of grass stubble at the time of flight. Beetles in flight have been observed, when flying over a relatively bare surface at dawn, to drop from about 10 ft. to 1 ft. or so above the surface in a spiralling descent. Sometimes a beetle would circle the bare surface a number of times and then fly up to about 10 ft. again and resume its flight, and sometimes a beetle would alight on the ground near some straw and burrow under it into the soil. This circling flight was never observed over stubble. These observations suggest that beetles are sometimes, at least, attracted to relatively bare areas in which they subsequently lay their eggs. Such behaviour can, of course, be observed only at dusk and at dawn. During the night, adults may still be attracted to relatively bare surfaces or they may aggregate in such places because these are the only ones from which they are not stimulated to fly.

There is a wealth of information which indicates that aggregations of adults occur in relation to moisture in the soil. For example, aggregations of larvae of *A. tasmaniae* are common along flinty outcrops where the soil receives much run-off, and depressions in pastures are often heavily infested with the larvae, particularly after dry summers. After wet summers, larvae are more numerous in areas which had bare surfaces in summer but are more widely distributed within such areas than after dry summers and, in undulating country, they are found

on the slopes and the tops of the rises; larvae can then even be numerous in places covered with stubble at the time of flight. There can be little doubt that the extended distribution of larvae after wet summers is mainly the result of larger numbers of females surviving to lay a larger number of eggs. Similarly, the occurrence of *A. tasmaniae* on different soil types is related to the wetness of the summer and the soil type.

In view of the necessity of water in soil for survival of the adults and for oviposition, it is suggested that the relatively bare surface of pastures in which adults aggregate is a 'token' stimulus. It is difficult to conceive how the adults could benefit from the bareness of the soil; the soil under a bare surface, however, commonly retains more water than soil under a dense stubble of perennial grass (Table III) and moreover is usually more easily wetted by light to medium showers of rain. Except perhaps in wet summers, adults should therefore survive in largest numbers and lay most eggs in places with bare surfaces.

The responses of beetles to water in soil, type of surface and shelter are not sufficient, however, to explain the aggregations of larvae which frequently occur in one particular type of place, namely, around haystacks, sheds, trees and other conspicuous objects. To explain the probable aggregation of adults around such objects Carne (1956) suggested that adults of *A. tasmaniae* orientate visually to objects on the horizon as do adults of some other scarabs, e.g., *Lepidiota caudata* (Smith, 1936) and *Melolontha melolontha* (L.) and *M. hippocastani* F. (Schneider, 1952). The available evidence suggests, however, that they do not do so. The direction of flight of *L. caudata* was thought not to be affected by wind direction (Smith, 1936) and *M. melolontha* and *M. hippocastani* sometimes flew with the wind, sometimes against the wind, and sometimes across the wind (Schneider, 1952). Adults of *A. tasmaniae*, except when they were flying to dung, flew apparently at random if it was calm and flew downwind, irrespective of the wind direction, if there was any wind. This behaviour is not suggestive of visual orientation to objects, and the following observations suggest that aggregations of adults around objects may occur in another way.

For all practical purposes only one flight occurred in the flight season of 1955. The beetles emerged after a thunderstorm and flew with a northerly wind on the nights of 11-13th February before laying any eggs. The incidence of larval damage around prominent objects in the winter of 1955 can be summarised as follows:— damage was most extensive around trees; sheds had comparatively few larvae around them. A few trees had sheltered sheep and were completely surrounded by extensive pasture damage; the bulk of the damage was usually found, however, on the northern side of the trees. Under the trees not completely ringed with pasture damage, the damage was usually under the outer edge of the canopy of leaves, and usually a belt of damage followed the outline of the canopy. In addition, the extent of the damage under these trees was related roughly to the height, width and density of the trees; stumps and ring-barked trees had no greater damage in their immediate vicinity than occurred in the pasture generally.

These observations suggest that beetles collided with the canopies of trees, fell to the ground immediately under them and burrowed into the soil. Beetles often collide with observers, particularly after dark, and it is not difficult to imagine how collisions could lead to an aggregation of adults. If a beetle is allowed to fly in a room, with a dim light to observe it by, it flies until it collides with a wall; it rebounds from the wall and strikes it again 2-3 ft. from where it collided from the previous time. This may occur a number of times, but usually the beetle falls to the ground after 3-5 collisions. A tree has a very large number of surfaces, i.e., a large 'total effective surface' with which a beetle can collide; if a beetle flies into a dense tree it is likely to fall to the ground before it flies out again. But if a beetle hits a brick wall of a width and height similar to that of the tree it could very well be free to carry on flying in its initial

direction after two or three collisions with the surface of the wall, i.e., the total effective surface of a wall is small. The number of beetles which accumulate around an object could thus be determined by the total effective surface which the object intrudes into their path of flight.

The general occurrence of larval damage around trees in 1955 was undoubtedly related to the direction of flight of the adults; similarly, in undulating country, most pasture damage occurred on slopes facing north or north-east. In some years, patches of larval damage have occasionally been seen on the eastern or western sides of isolated trees, but larval damage around trees and other conspicuous objects has only been prevalent and widespread when thunderstorms have stimulated the emergence of beetles; and then, as in 1955, the damage has usually been restricted to the northern side of the objects.

The prevalence of *larvae* on the northern sides of objects does not necessarily mean that aggregations of *beetles* are prevalent only on the northern sides of objects. When the beetles fly with a northerly wind it is usually to be expected that the females either are (a) females which have recently emerged after rain brought by a tropical thunderstorm and have not laid their first batches of eggs, and so are capable of laying these eggs in places in which they aggregate; or (b) fully-fed, gravid females capable of laying the second batches of eggs. When, however, the beetles fly with a wind from any other direction the females usually either are (a) females which have emerged after rain brought by a cold front and have laid their first batches of eggs before flying; they, furthermore, have some fat-body but have not fed on dung (Table II) and are not capable of laying any eggs until they *have* fed on dung; or (b) fully fed gravid females which are capable of laying their second batches of eggs. Aggregations of *larvae* cannot, of course, result from aggregations of females which are not capable of laying eggs until they have fed on dung, unless there happens to be sufficient dung in the places in which the females happen to aggregate. This, indeed, may occasionally happen if these particular sorts of females aggregate near trees under which sheep are 'camped' or have recently 'camped', and may explain the occasional aggregations of *larvae* on other than the northern sides of objects. However, since, in addition, the first batches of eggs probably constitute about 70 per cent. of the total of eggs laid, it is clear that aggregations of *larvae* are most likely to occur when the sequence of events has led adults to aggregate on the northern sides of objects.

If, however, beetles *do* aggregate around conspicuous objects by chance collisions after dark, then it is probable that such aggregations *do* occur most frequently on the northern side of objects. When the beetles fly with a north wind the night is usually warm and large numbers of beetles fly throughout the night, whereas when the beetles fly with any other wind the nights are usually colder and beetles cease flying soon after dark. The probability of collision with objects would therefore be highest when the beetles flew with a north wind. Moreover, when a north wind is blowing, the sky is usually cloudy and the night is dark; but on other nights when flight is possible the sky is cloudless and the night is relatively bright. It is also possible that beetles only collide with conspicuous objects on dark nights and *avoid* such objects when the sky is bright at night. That this may be so is suggested by an observation by P. B. Carne (private communication) that beetles in flight veered away from an upright post in their path of flight.

Summary.

In the lower South-East of South Australia, adults of *Aphodius tasmaniae* Hope, which is an economic pest of improved pastures, emerge from the soil 2-3 days after rain has fallen in summer. The females may lay two batches of eggs. The first batch (about 35 eggs) is developed at the expense of the fat-body

and is laid 3-6 days after emergence; a second batch (about 20 eggs) can be developed and laid after the female has fed on dung.

The beetles are crepuscular and fly after sunset if the weather is suitable for flight. The first batch of eggs may or may not be laid before flight, depending on the weather. Until the fat-body is largely depleted, beetles fly with the wind and are attracted to lights, but after that stage has been reached they fly upwind to dung and are not attracted to lights. After feeding on dung for a few days the females become gravid again, and apparently change their responses to light and wind once more. The distribution of larvae in the field suggested that adults aggregated and laid eggs in specific places. The factors which promote aggregations of adults were therefore studied.

The survival-rate of the females and the number of eggs they laid in two soils, a sand and a clay loam, were related to the 'available water' in soil as measured by the pF scale. Females survived in largest numbers and laid most eggs in the range of pF 2.8-3.2 in both soils. Similarly, when given a choice of a number of water contents in soil, beetles aggregated in largest numbers within the range 2.8-3.2 in one soil and pF 2.8-3.5 in another. In the latter soil, however, the pF values that were tested were more widely spaced, and it is suggested that the combined data are only intelligible if there was an optimum range of pF within the vicinity of 2.8-3.2 in both soils. These and other experiments indicated that moisture in soil was the major factor capable of promoting aggregations of adults.

When water was not limiting, aggregations of beetles occurred on loose as opposed to compact surfaces. However, 'shelter' (dry grass stems broken off the parent plant, dung, etc.) was capable of promoting aggregations even if the soil underneath ordinarily inhibited burrowing. Aggregations of beetles also occurred on surfaces into which other beetles had previously burrowed; this was probably due not to any attraction of beetles to other beetles, but to loosening of the surface soil by the original beetles, which permitted later arrivals to burrow rapidly.

It is probable that the patchy distribution of larvae in the field is due to the aggregation of the adults in the field mainly in relation to moisture in soil, type of surface and shelter. It is also suggested that aggregations of larvae that occur around conspicuous objects, such as trees, result from beetles colliding with these objects by chance when they are flying after dark, dropping to the ground and burrowing into the soil to lay eggs there.

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References.

- CARNE, P. B. (1956). An ecological study of the pasture scarab *Aphodius howitti* Hope.—*Aust. J. Zool.* **4** pp. 259-314.
- EVANS, A. C. (1944). Observations on the biology and physiology of wireworms of the genus *Agriotes* Esch.—*Ann. appl. Biol.* **31** pp. 235-250.

- EVANS, A. C. & GUILD, W. J. McL. (1948). Studies on the relationships between earthworms and soil fertility. IV. On the life cycles of some British Lumbricidae.—*Ann. appl. Biol.* **35** pp. 471–484.
- GIVEN, B. B. (1958). A note on the status of *Aphodius tasmaniae* Hope.—*Proc. Linn. Soc. N.S.W.* **83** p. 196.
- LEES, A. D. (1943). On the behaviour of wireworms of the genus *Agriotes* Esch. (Coleoptera, Elateridae). II. Reactions to moisture.—*J. exp. Biol.* **20** pp. 54–60.
- MADGE, P. E. (1952). The pasture cockchafer in South Australia.—*J. Dep. Agric. S. Aust.* **55** pp. 463–467.
- MARTYN, E. J. (1950). Pasture insects investigations. Report on the occurrence of pasture cockchafers in Tasmania, 1949–50.—*Tas. J. Agric.* **21** pp. 216–221.
- SCHNEIDER, F. (1952). Untersuchungen über die optische Orientierung der Maikäfer (*Melolontha vulgaris* F. und *M. hippocastani* F.) sowie über die Entstehung von Schwärmbahnen und Befallskonzentrationen.—*Mitt. schweiz. ent. Ges.* **25** pp. 269–340.
- SMITH, J. H. (1936). White grub damage to pastures on the Atherton Tableland. *Qd agric. J.* **46** pp. 446–467.
- SWAN, D. C. (1934). A scarab beetle (*Aphodius tasmaniae*, Hope) destructive to pastures in the south-east of South Australia.—*J. Dep. Agric. S. Aust.* **37** pp. 1149–1156.
- SWEETMAN, H. L. (1931). Preliminary report on the physical ecology of certain *Phyllophaga* (Scarabaeidae, Coleoptera).—*Ecology* **12** pp. 401–422.



FIG. 1. The contrast between a pasture with a bare surface (background) and a pasture covered with dense stubble (foreground). The pasture in the background has been cut for grass hay and has the type of surface on which adults of *A. tasmaniae* aggregate and lay eggs. Photograph by Mr. K. P. Phillips, Mil-Lel, October 1949.



FIG. 2. Close-up of a relatively bare surface in summer; on such surfaces adults of *A. tasmaniae* tend to aggregate.



FIG. 3. A sheep 'camp' along a fence showing the type of surface on which adults of *A. tasmaniae* aggregate. Mt. Schanck is in the background. March 1955.

NOTES ON THE GENUS *HETEROCOCCUS* FERRIS (COCCOIDEA, HOMOPTERA) WITH A DESCRIPTION OF A NEW SPECIES INJURIOUS TO GUINEACORN (*SORGHUM VULGARE*) IN NIGERIA.

By D. J. WILLIAMS

Commonwealth Institute of Entomology.

The genus *Heterococcus* was erected by Ferris (1918) for a new species, *H. arenae* Ferris, having 9-segmented antennae, a denticle on the claw and with the normal trilocular pores replaced by quinquelocular pores. Other species were added later and Morrison (1945) discussed the genus at some length and described in detail three other related genera.

Two of these, *Laingiococcus* Morrison and *Annulococcus* James, differ from *Heterococcus* and *Asphodelococcus* Morrison in possessing 1-4 circuli. *Asphodelococcus* differs from *Heterococcus* in having 6-segmented antennae, a few trilocular pores and no multilocular pores.

Some specimens of a mealybug doing considerable damage to guineacorn (*Sorghum vulgare*) in Nigeria have been received from Mr. K. M. Harris and these represent a new species showing some surprising characters. About half of the specimens have a small but distinct circulus, the antennae are mainly 8-segmented, there is no denticle on the claw and some trilocular pores are present around the abdominal cerarii and spiracles. However, as this species bears an obvious relationship to *Heterococcus* in other ways it seems desirable to describe it in this genus rather than place it in any other genus.

Existing descriptions of the single British species of *Heterococcus* are unsatisfactory, partly because the type specimens are in a poor state, and the opportunity is taken to redescribe this species from some excellent material kindly made available by Dr. K. L. Boratynski, Imperial College of Science and Technology, London.

***Heterococcus nigeriensis* sp. n. (fig. 1).**

Recognition characters. Shape elongate oval, length approximately 3.5 mm., anal lobes poorly developed. Antennae small, usually 8-segmented, rarely 9-segmented or with terminal segment partly divided. Legs slender in comparison to size of body, claw without a denticle, posterior tibiae and femora with small translucent pores. Circulus present or absent, when present lying between fourth and fifth segments and exceedingly small. Ostioles present as poorly developed posterior pair only, lips each with 2-4 trilocular pores. Anal ring situated a very short distance from apex of body, not joined anteriorly; with 6 setae slightly longer than diameter of ring and with a double band of pores. Cerarii on last 2 segments only, each with a pair of short lanceolate setae accompanied by 3-4 trilocular pores, the cerarian setae only slightly larger than other surrounding setae. Dorsal setae not numerous, very small and lanceolate. Multilocular disc pores in transverse rows at posterior edges of last few abdominal segments but more numerous in submarginal groups which also extend to head; anteriorly they form a more or less continuous band. Quinquelocular disc pores rather numerous over entire surface. Trilocular pores in a single transverse row in the middle of some of the posterior abdominal segments, these smaller than quinquelocular pores. Tubular ducts slender, not numerous, situated only among the submarginal groups of multilocular disc pores on abdomen.

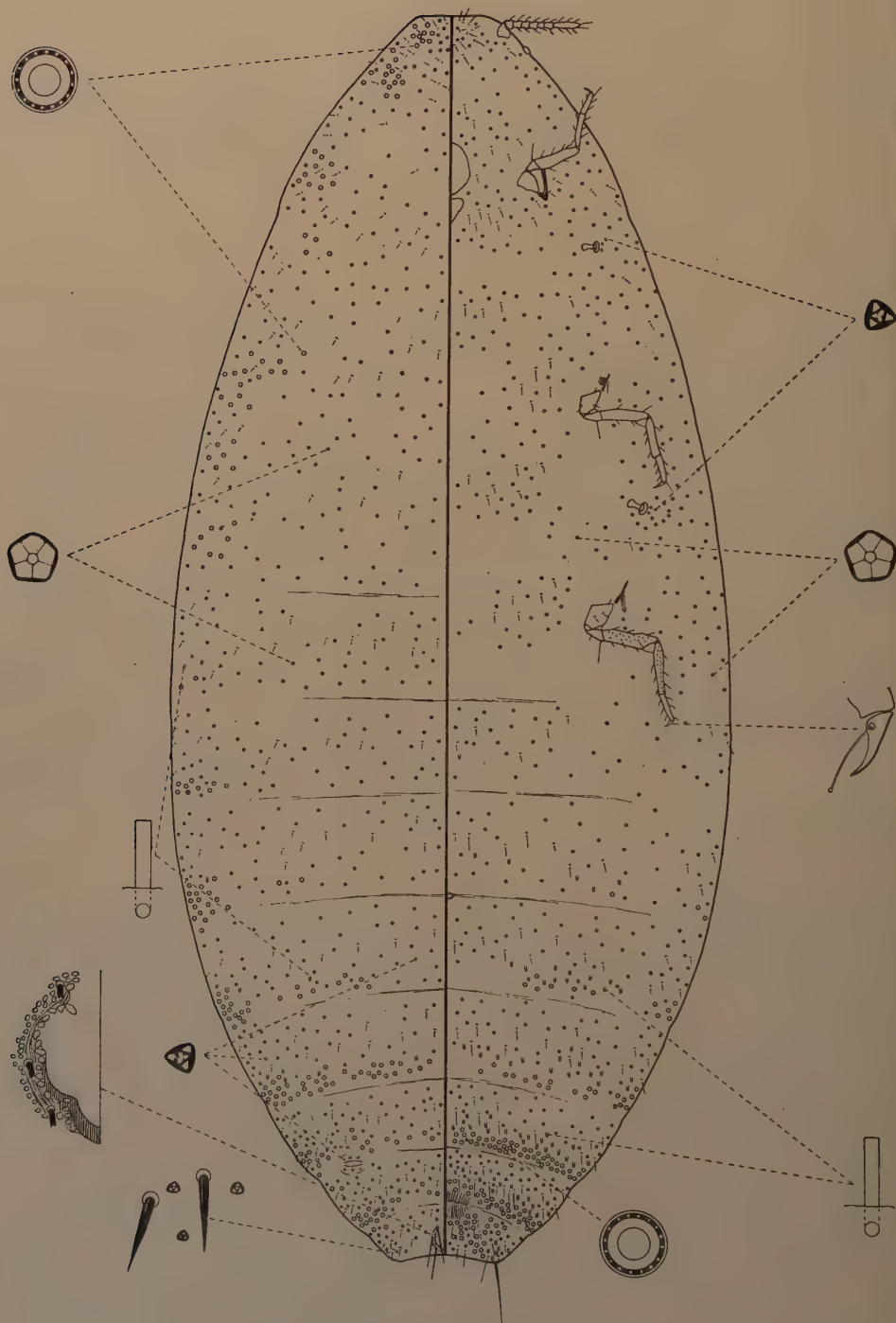


Fig. 1.—*Heterococcus nigeriensis* sp. n.

Ventral surface with anal lobe setae about twice as long as anal ring setae. Ventral setae slender but longer than those on dorsum, not numerous. Multilocular disc pores arranged in transverse rows at posterior edges of fifth and posterior segments and becoming more numerous posteriorly. Quinquelocular disc pores evenly distributed. Trilocular pores numbering 2-3 near each spiracular opening. Tubular ducts in transverse rows on fourth and posterior segments.

On guineacorn (*Sorghum vulgare*) causing severe distortion. NIGERIA: Samaru, (K. M. Harris) 19.vi.1958, 27.vi.1958, 7.v.1959.

Notes. The mealybugs causing the damage are stated to be yellowish pink and to be found between the stem and leaf sheath, or in the rolls of deformed leaves, of *S. vulgare* (Harris, 1961). It has been impossible to separate these mealybugs on morphological grounds from others that are stated to be mid-grey and to feed only on the expanded leaves of *Sorghum*, without causing deformation. In both forms, a circulus may be present or absent. Whilst it seems doubtful that more than one species is involved, field evidence suggests the possible existence of two biological races, and for this reason a specimen sent as representing the pink form has been selected as the holotype.

The only specimens seen by the writer have been taken from *S. vulgare*, but Harris (*op. cit.*) indicates that symptoms similar to those caused on *Sorghum* occur on *Zea mays*, *Cynodon dactylon*, *Pennisetum typhoides* and *Chloris pycnothrix*.

The species is similar to *H. pulverarius* (Newstead) redescribed below but differs in lacking the denticle on the claw, in possessing 8-segmented antennae and a few trilocular pores on the dorsum and around the spiracles. Although not a constant character the circulus is often present, a condition not found in any other species of *Heterococcus*.

The holotype is deposited in the British Museum (Natural History).

***Heterococcus pulverarius* (Newstead) (comb. nov.) (fig. 2).**

Ripersia pulveraria Newstead (1892, p. 145).

Phenacoccus nudus Green (1926, p. 172) (syn. nov.).

Heterococcus nudus (Green) (Green, 1928, p. 21).

Heterococcus nudus (Green) (Morrison, 1945, p. 53).

Habit. Described originally as pale pink from between the stem and leaf sheath of *Agrostis vulgaris* at Sandiway, Cheshire, England and later by Green as pale orange-yellow beneath the ensheathing bases of the leaves of grasses at Camberley, Surrey, England. In both cases the adult female is described as dusted with powdery secretion but without waxy tassels.

Recognition characters. Adult female elongate oval attaining a length of 4 mm., anal lobes moderately developed. Antennae 6-, 7- or 9-segmented. Legs slender, claw with a distinct denticle, hind tibiae and femora with translucent pores. Circulus absent. Anterior and posterior pairs of ostioles present, poorly developed, the lips each with about 3 quinquelocular pores and an occasional seta. Anal ring situated at apex of body, with 6 setae about twice as long as diameter of ring. Cerarii recognisable on anal lobes and penultimate segment, each with 2 lanceolate setae which are only slightly larger than dorsal setae and accompanied by about 3-5 quinquelocular pores; single setae resembling cerarian setae on sixth and seventh segments and ocular cerarius sometimes discernible with 3 setae. Trilocular pores absent. Dorsal setae minute and lanceolate, not numerous. Multilocular disc pores in single transverse rows on posterior edges of posterior abdominal segments and also in submarginal groups around the body including the head, tending to be more numerous on prothorax and head. Quinquelocular disc pores not numerous, evenly distributed and noticeably larger towards margins and especially on margins of posterior segments and around the cerarii. Tubular

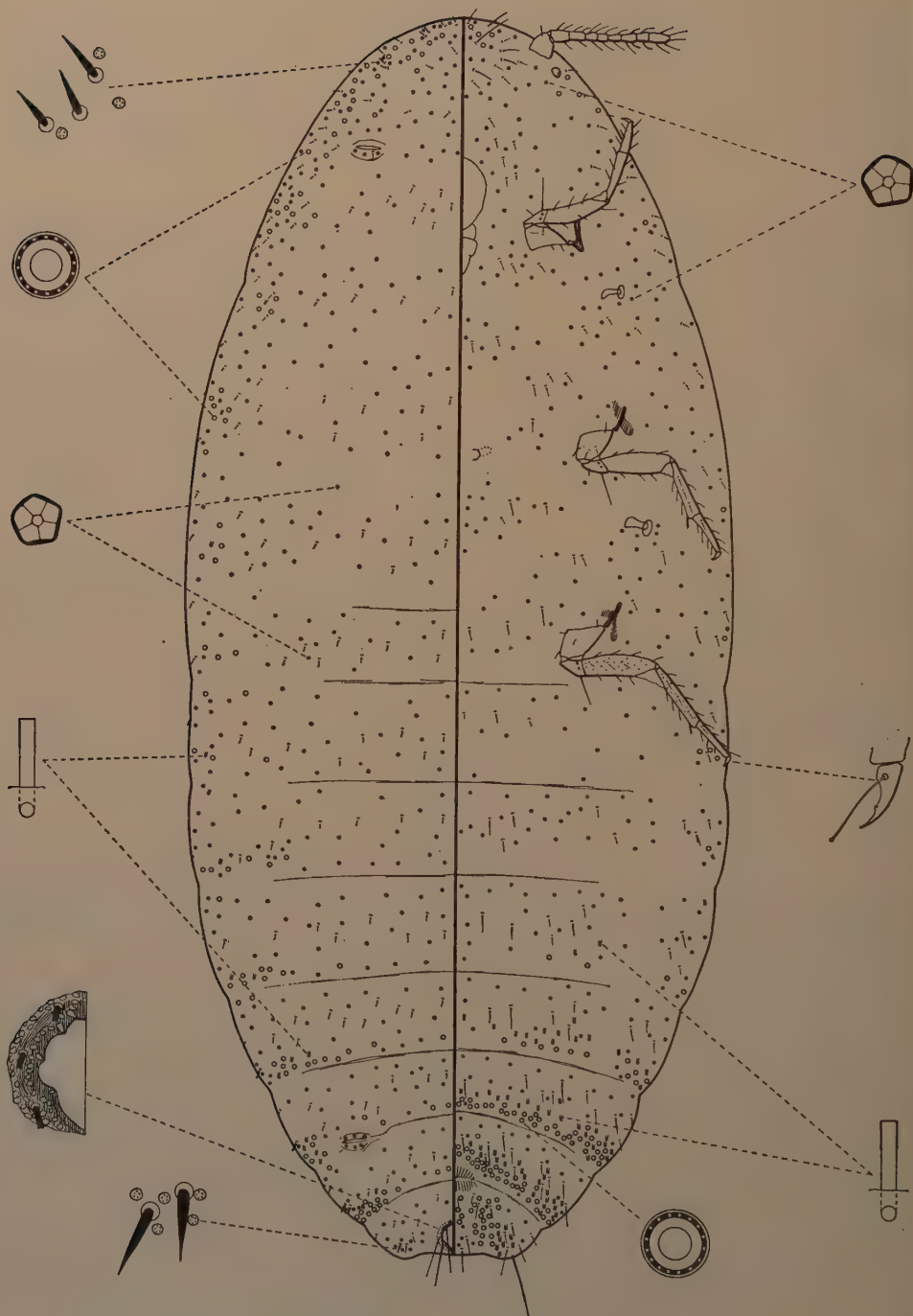


Fig. 2.—*Heterococcus pulverarius* (Newstead).

ducts slender, there being 1-4 among each of the submarginal groups of multilocular disc pores but absent on head.

Ventral surface with anal lobe setae about twice as long as anal ring setae. All ventral setae slender but longer than dorsal setae. Multilocular disc pores present in transverse rows on fifth and posterior segments; on the seventh and eighth segments forming double or triple rows at posterior edges; small submarginal groups also present, which extend to the head. Tubular ducts, similar to those on dorsum, in transverse rows on sixth to eighth segments and also on anal lobes, there being also occasional ducts on some anterior segments especially around the margins. Quinquelocular disc pores sparse.

Notes. In the type specimens of *Ripersia pulveraria*, the antennae are either 6- or 7-segmented but most of the specimens are parasitised. In other respects they are identical with specimens of *Phenacoccus nudus* Green with 9-segmented antennae, and the reduction in number of antennal segments of Newstead's material is probably due to parasitism. Since Newstead described the species the name has been given in error to more than one species of *Trionymus* by both Newstead and Green under the generic names *Dactylopius*, *Pseudococcus* and *Trionymus*. Only Newstead's original type material refers to this species.

The accompanying figure has been drawn from material collected by Dr. K. L. Boratynski at Silwood Park, Berkshire, England, and differs slightly from the type material of *Ph. nudus* in having fewer multilocular disc pores, especially on the dorsal side of the head.

Inadequate descriptions of this species, and in particular regarding the length of the cerarian setae, have led Morrison (1945) to give incorrect key characters. In the same paper Morrison described as new *H. graminicola*, a species which may be the same as *H. pulverarius*.

It is interesting that Schmutterer (1958) has described *Heterococcus variabilis* from material collected in Germany and Holland with antennae 6- to 9-segmented and it is possible that this species is also the same as *H. pulverarius*.

References.

- FERRIS, G. F. (1918). The California species of mealy bugs.—*Leland Stanf. Univ. Publ. Univ. Ser.*, 78 pp.
- GREEN, E. E. (1926). Observations on British Coccidae. X.—*Ent. mon. Mag.* **62** pp. 172-183.
- GREEN, E. E. (1928). Observations on British Coccidae. XI.—*Ent. mon. Mag.* **64** pp. 20-31.
- HARRIS, E. (1961). Distortion of guineacorn (*Sorghum vulgare*) caused by a mealybug, *Heterococcus nigeriensis* Williams, in Northern Nigeria.—*Bull. ent. Res.* **51** pp. 677-684.
- MORRISON, H. (1945). The mealybug genus *Heterococcus* Ferris and some of its relatives (Homoptera: Coccoidea).—*J. Wash. Acad. Sci.* **35** pp. 38-54.
- NEWSTEAD, R. (1892). On new or little known Coccidae, chiefly English (No. 2).—*Ent. mon. Mag.* **28** pp. 141-147.
- SCHMUTTERER, H. (1958). *Heterococcus variabilis* n. sp., eine neue Pseudococcide mit bemerkenswerter Variabilität (Homoptera: Coccoidea, Pseudococcidae).—*Acta faun. ent. Mus. nat. Pragae* **3** pp. 17-22.

DISTORTION OF GUINEACORN (*SORGHUM VULGARE*) CAUSED BY A MEALYBUG, *HETEROCOCCUS NIGERIENSIS* WILLIAMS, IN NORTHERN NIGERIA.

By ELIZABETH HARRIS

E.M.V.

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(PLATE XVIII.)

In June 1954, many plants in a field of guineacorn (*Sorghum vulgare*) at Samaru, in Northern Nigeria, were deformed and stunted. This condition, which was named 'distortion', was frequently seen on guineacorn and maize (*Zea mays*) during the next four years and was also found on the grass weed, 'dhub' (*Cynodon dactylon*), growing amongst affected cereal crops.

Distortion has not been reported previously but is well known to local farmers who call it 'kuturu' (leprosy, a general term also applied to the downy mildew diseases of guineacorn and bulrush millet, *Pennisetum typhoides*, caused by *Sclerospora* spp.). It often causes considerable loss of stand on local farms, many guineacorn plants remaining a few inches high for months and finally rotting, while others which recover are retarded. In badly infested fields, where stands are hoed out and resown, the new seedlings often become affected soon after emergence, and if seedlings showing distortion symptoms are removed during thinning the remaining plants in that stand usually become affected later.

Repeated attempts to discover the cause of distortion failed. The possibilities of the causal organisms being fungi, bacteria, nematodes or aphids were considered but there was no constant association between distortion and any of these, and the fact that plants frequently recovered from distortion made it unlikely that a virus was concerned.

Finally, in June 1958, a few mealybugs were found under the leaf sheaths of guineacorn plants showing distortion symptoms. Three of these mealybugs were transferred to a healthy guineacorn seedling, which developed severe distortion within nine days. In subsequent dissections of affected plants, mealybugs or signs of their waxy secretions were always found. The study of distortion of guineacorn and the mealybug which causes it are reported in this paper.

Symptoms.

The symptoms of distortion observed in guineacorn, maize and dhub are striking and readily recognised. Affected leaves and leaf sheaths become severely mis-shapen, apparently by abnormal growth of the tissue between the veins, which is shorter and wider than normal, so that the veins are irregularly divergent and undulating instead of parallel. The abnormal tissue between the veins is white, and the normal green colour is restricted to the veins, which are wider than in healthy leaves. Affected stems are much shorter and wider than normal and in some cases hollow pegs or solid outgrowths of the main vascular bundles occur on the stems, leaf sheaths or leaves. The symptoms seen in the field vary from small areas of distortion on single leaves to plants with severe distortion of stem, leaf sheaths and leaves. When small areas of leaf tissue are affected, normal growth continues although the unfolding leaves may be constricted for a short time. In severely affected plants, however, the abnormal leaf and leaf-sheath tissue is unevenly crumpled, and the leaves do not unfurl but remain rolled

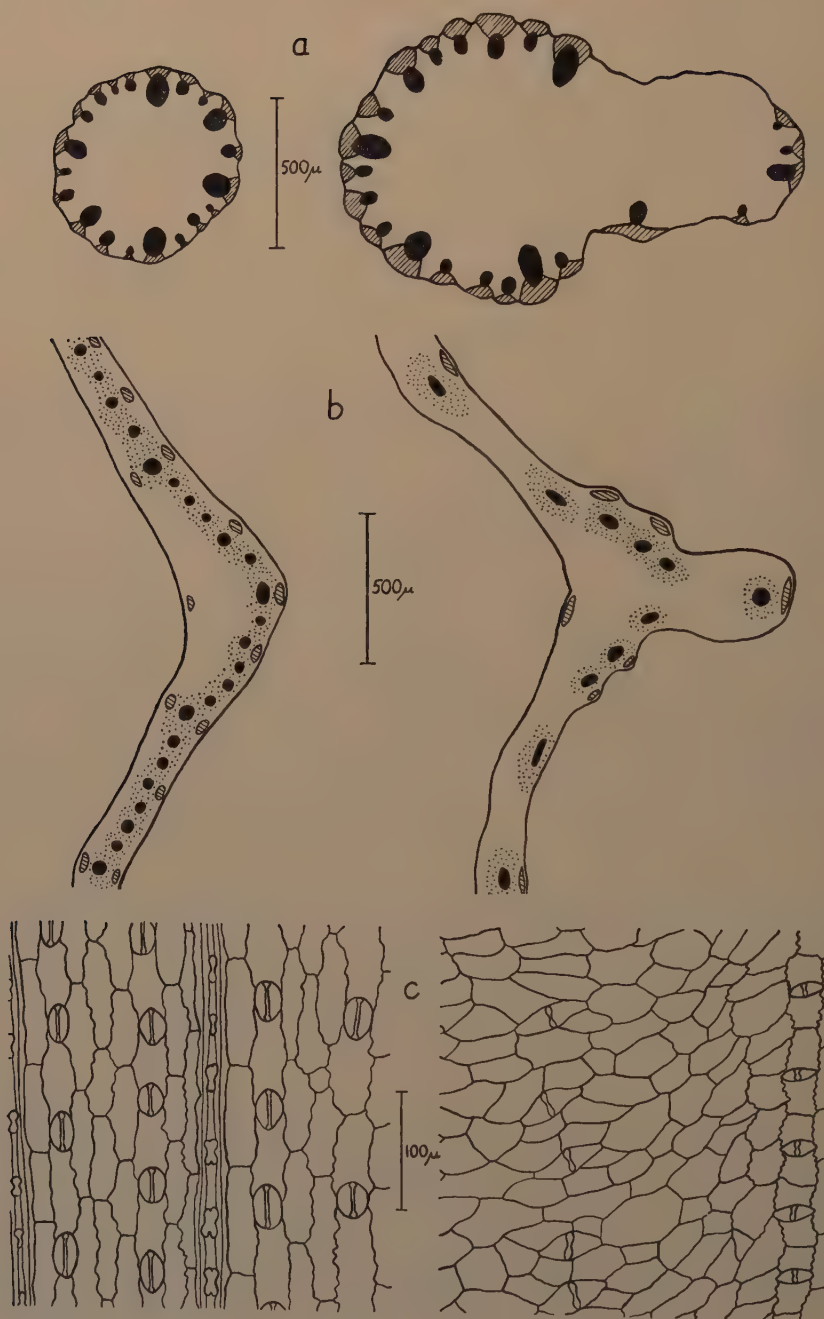


Fig. 1.—The anatomy of plants of *Cynodon dactylon* showing symptoms of distortion associated with the presence of a mealybug, *Heterococcus nigeriensis*: a, diagrammatic cross sections of normal and distorted flowering stems; b, diagrammatic cross sections of normal and distorted leaves (midrib in centre); c, lower epidermis of normal and distorted leaves (camera lucida drawings). In all cases the normal material is on the left. In a and b the black areas represent vascular bundles, the shaded areas sclerenchyma and the dotted areas tissue containing chloroplasts.

together. Such plants are thick at the base and stunted and the crumpled roll of leaves in the centre is often bent horizontally and twisted (Pl. XVIII, fig. 1).

If the mealybugs causing the distortion die or leave the plant, the stem elongates and healthy leaves are produced which eventually force their way out of the twisted roll of abnormal leaves, often remaining held at the tip so that subsequent leaves form a series of arches. When mealybugs remain on the plant, there is little or no growth, and the new leaves are deformed and borne on such short stem internodes that they are unable to break out of the roll of abnormal leaves. Guineacorn plants which make no new growth usually rot after some months, but maize plants affected by distortion for much of the growing season have been collected at harvest time. These had stems under 1 ft. long (stems of healthy plants of the same crop being about 6 ft. long) and bore tassels and one or two small cobs with a few grains in each (Pl. XVIII, fig. 2). Plants may be affected at all stages of development but distortion is most common during the first two months of the growing season. Symptoms of distortion developing on guineacorn seedlings during laboratory experiments with the mealybugs (Pl. XVIII, fig. 3) were identical with those on plants in the field. A distinction was made in this case between severe distortion, where the damage had the appearance of being systemic (affecting large areas of tissue), and mild distortion, where the effects were limited to small parts of the leaf or coleoptile as bumps or hollow pegs.

The anatomy of plants showing distortion symptoms has not been studied in detail, but diagrams of cross sections of affected and normal leaves and stems of *C. dactylon* (fig. 1) show considerable disorganisation of the tissues. (*C. dactylon* was used in these studies because, in the greenhouse, it could be more easily maintained than guineacorn. The distortion symptoms were induced by mealybugs from affected guineacorn.) The flowering stem affected by distortion is much wider than the healthy flowering stem and has an irregular outgrowth on one side (fig. 1a). Both the stems from which these sections were cut bore flowering heads at the same stage of development but whereas the length of the normal stem was over 15 cm. that of the deformed stem was under 2 cm. In the affected leaf (fig. 1b) the vascular bundles are oval in cross section, separated by varying amounts of abnormal parenchyma made up of large thin-walled cells without intervening air spaces, and chloroplasts are confined to the areas round the vascular bundles. The epidermal cells over the abnormal parenchyma between veins of an affected leaf are irregular in shape and arranged haphazardly and the guard cells of the stomata are widened to a spindle shape (fig. 1c).

Plant species affected by distortion.

Distortion has been observed on the following cereals and grasses in the field:—*Sorghum vulgare*, common, particularly at the beginning of the growing season.

Zea mays, often very severe at the beginning of the growing season.

Cynodon dactylon, common throughout the growing season in fields where guineacorn or maize is affected.

Chloris pycnothrix, on one plant only.

Pennisetum typhoides, once, on two adjacent seedlings.

In the greenhouse, symptoms of distortion which are identical with those observed in the field have been induced by transferring mealybugs from affected guineacorn plants on to *Zea mays*, *Cynodon dactylon* and *P. typhoides*. This strongly suggests that the same species of mealybug is causing distortion in all of these hosts, but, at present, collections of mealybugs from hosts other than guineacorn have not been submitted for identification.

Distortion has also been induced in the greenhouse on *Triticum aestivum*, *Oryza sativa* and *Digitaria exilis* by mealybugs transferred from guineacorn, but the condition has not been observed on any of these hosts in the field.

Distortion has been seen in many localities around Samaru and also at Kano, Zuru and Ilorin. It seems likely that it occurs throughout Northern Nigeria.

Mealybugs.

Mealybugs from affected guineacorn plants were submitted to Dr. D. J. Williams of the Commonwealth Institute of Entomology, who has described them as a new species, *Heterococcus nigeriensis* Williams (1961). The insects are oval and yellowish pink with a white waxy covering. They are found (usually in small numbers) under the leaf sheaths, in the roll of deformed leaves or occasionally round the roots of plants showing symptoms of distortion but have not been found on healthy plants. The nymphs are active but the adults move very little. Eggs are laid in large numbers, usually under the leaf sheaths, surrounded by waxy filaments secreted by the female, and the nymphs emerge after about five days. Ants are frequently present on the mealybug-infested plants but they are tending aphid colonies and have not been seen in contact with the mealybugs, which may be inaccessible to them.

The inherent ability of the mealybugs to cause distortion without having fed from an affected plant was shown by rearing mealybugs from the egg on healthy seedlings. Three such mealybugs caused mild distortion symptoms on a seedling within two weeks of the eggs being placed on it.

Attempts made to establish mealybug colonies on sprouting potato tubers were not successful; adult mealybugs would not settle on the shoots and although newly hatched nymphs appeared to feed, the shoots became necrotic within a few days and the nymphs died. Most of the mealybugs for the experiments were collected in local farms from plants showing severe distortion symptoms but later it was found possible to maintain colonies in the greenhouse on dhub or guineacorn.

In 1958, several tillers of volunteer guineacorn in a field where distortion was common were heavily infested with mealybugs. In spite of the heavy infestation the tillers showed no symptoms of distortion. The mealybugs concerned could not be separated on morphological grounds from those causing distortion, but they exhibited marked differences in colour and behaviour; they were mid-grey with a white waxy covering and were present in large numbers on the expanded leaves but not under the leaf sheaths; they were tended by ants (*Pheidole* sp.) and the tillers were all within a few feet of the ants' nests. When these mealybugs (after up to 72 hours' starvation) were placed on the coleoptiles of guineacorn seedlings they moved off immediately and although they were replaced repeatedly none settled until the first leaves of the seedlings were expanded, when the survivors settled on the leaf blades. No distortion symptoms appeared subsequently on these seedlings but mild distortion symptoms were caused in one case by six small nymphs of this type feeding on the outside of the leaf sheaths of a maize seedling. It seems likely that the grey mealybugs do not cause distortion because they normally feed on leaves where growth has ceased, whereas the pink mealybugs feed on actively growing tissues.

Experimental methods.

As the symptoms of distortion appear rapidly, it was possible to investigate the condition by feeding mealybugs on seedlings growing in test-tubes. Guineacorn seedlings grew satisfactorily under these conditions and were used in all the feeding tests; equal numbers of control seedlings were grown under identical conditions at the same time. Clean grain was put to germinate on moist filter paper in petri dishes, and, after 24 hours, healthy seedlings with plumules already growing were selected, the radicles were wrapped in absorbent cotton-wool and each seedling was placed in a small specimen tube containing enough distilled water to moisten the cotton-wool. The tubes were corked and kept near a window

for up to 24 hours before introducing the mealybugs. Mealybugs were collected from plants with severe distortion symptoms and starved for 48 hours in covered watch-glasses. In all experiments one mealybug was placed on each test seedling. Each mealybug was measured under the binocular microscope, placed on the shoot of a seedling (using a moist camel-hair brush) and subsequently watched and replaced if it moved off the shoot. The time between the last replacement and the removal of the mealybug, which was done after a prearranged interval, was taken as the presumed feeding time (P.F.T.). After removal of the mealybugs from the test seedlings, all the seedlings, including the controls, were dipped in malathion (1 part 40 per cent. emulsifiable concentrate in 200 parts water) and transferred to test-tubes ringed with vaseline and covered with circles of fine lawn held on by rubber bands. All the glassware was washed in a detergent solution and rinsed well before use and the lawn circles and specimen-tube corks were fumigated in ethyl acetate vapour.

Results.

Distortion symptoms appeared on the test seedlings very soon after the mealybugs fed. The first sign of distortion was an abrupt cessation of the normal elongation of the plumule (fig. 2) and within the next two days the deformed leaves

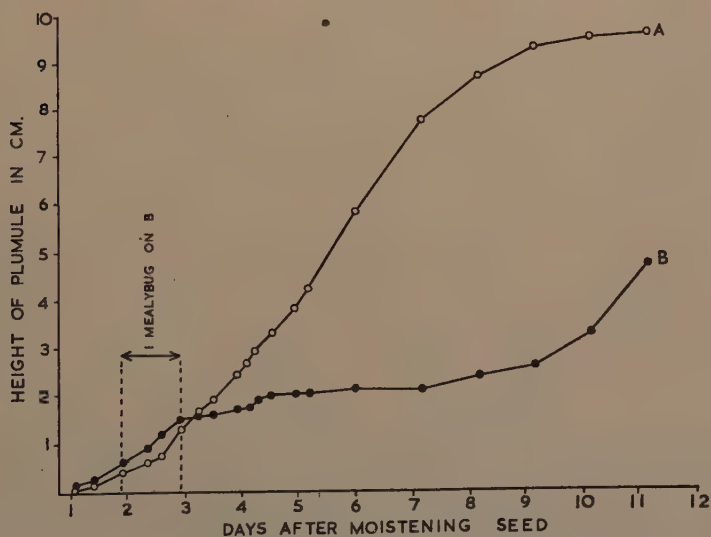


Fig. 2.—Growth curves of guineacorn seedlings (in test-tubes). A, mean of 8 control seedlings; B, seedling with severe distortion after a mealybug had been placed on it for a P.F.T. of 24 hr.

became visible. Distortion of the coleoptile or the blade of the first leaf was often visible by the time that the mealybugs were removed but when the sheath of the first leaf or any part of subsequent leaves was affected this was not visible until later, when the deformed tissues broke out of the normal leaves surrounding them. The appearance of seedlings six days after feeding of a single mealybug is shown in Plate XVIII, fig. 3.

The results of the feeding tests are shown in Table I. The shortest P.F.T. to produce symptoms was one of 7 hours' duration and in this case the symptoms were of severe distortion. There is some evidence of variation in the ability of the mealybugs to produce distortion; in tests between 9th and 23rd May, mealybugs 1 mm. or over in length caused severe distortion, and mild distortion was only caused by mealybugs less than 1 mm. long, but in later tests mealybugs from 1 mm. to 2 mm. long often caused only mild distortion. No distortion symptoms occurred on any of the control seedlings.

TABLE I.

Distortion caused by single mealybugs on guineacorn seedlings.

Date	No. of test seedlings	Range of P.F.T. (hr.)	Seedlings developing distortion symptoms	
			severe	mild
23.iv.59	6	24	1	0
29.iv.59	4	24	0	0
9.v.59	7	23	4	0
10.v.59	5	26	1	2
15.v.59	6	7-22	3	0
21.v.59	13	21-23	1	5
22.v.59	5	24-28.	2	0
23.v.59	2	24	1	0
24.v.59	2	24	0	1
25.v.59	8	1-6	0	0
25.v.59	12	20-24	0	0
26.v.59	2	25-26	0	0
27.v.59	2	27	0	0
29.v.59	6	24	0	0
30.v.59	2	51	0	1
1.vi.59	2	48	0	1
6.vi.59	10	24-25	5	0
*25.viii.59	6	24	2	1
*28.xi.59	10	22-31	0	5
*30.xi.59	13	2 $\frac{1}{2}$ -6	0	0
	123		20	16

* Mealybugs from colonies in the greenhouse.

Affected seedlings were kept to observe subsequent development, and in every case recovery was apparent in the production of normal leaves in from 4 to 11 days after removal of the mealybugs. The length of time before a normal leaf was visible depended on the degree of mechanical obstruction due to the deformed leaves surrounding it; once free of this obstruction the growth of the seedlings was normal.

Both in plants from the field and in test seedlings, severe distortion had the appearance of being systemic. In particular it was noticed in dissecting affected plants that distortion symptoms occurred on unopened leaves which showed no signs of mealybugs or waxy secretions on the surface. It was, however, suspected that the mealybugs were inserting their stylets through several outer leaves to feed on the inner ones, and this was confirmed by feeding mealybugs on younger seedlings than usual and removing them before the first leaf started to emerge from the coleoptile. On several of these seedlings, distortion developed on the coleoptile and the first leaf and in one case on the second leaf also. When the

symptoms were of mild distortion the small patches of affected tissue on the leaves were in positions likely to have been directly below the affected part of the coleoptile when feeding occurred. Moreover, although symptoms of severe distortion had the appearance of being systemic, dissections of plants heavily infested with mealybugs showed that some normal leaves were always present inside the deformed leaves.

Attempts to reproduce the symptoms of distortion in healthy seedlings by mechanical transmission (rubbing the leaves with sap from affected plants and carborundum) and by grafting salivary glands of mealybugs into the coleoptiles were unsuccessful. When fragments of severely affected maize leaves were grafted into the leaves of maize seedlings, however, two out of five seedlings showed some irregular enlargement of the epidermal cells immediately around the graft, although there was no indication of further spread of the symptoms.

Discussion.

Distortion is unlike other toxic feeding effects caused by mealybugs in that severe symptoms appear immediately after single insects have fed for a short time. The symptoms also are quite different, resembling those caused by growth substances rather than toxins; in addition, the grey mealybugs (capable of producing distortion when they feed on meristematic tissue) produce no abnormal symptoms on mature tissue. When mealybugs were first found to be associated with distortion it seemed likely that the symptoms were due to infection by a mealybug-transmitted virus. The evidence of the feeding tests, however, particularly the immediate development of symptoms after feeding and the regular recovery after removal of the mealybugs, points to distortion being caused by some substance which is introduced into the tissues by the mealybugs as they feed and which radically affects further growth but does not cause wilting or death. In many respects distortion resembles a simple gall, the growth of which is stimulated by feeding. A plant with severe distortion may provide a more favourable environment for the mealybugs than does a healthy plant because the meristematic tissues on which the insects feed do not grow away from them and the deformed leaves give them increased protection.

Distortion is important on small plots of guineacorn and maize grown as food crops by peasant farmers where any method of chemical control of the mealybugs would not be economic or practicable. The improvement of cultural practices would probably give almost complete control of the mealybugs. Distortion is virtually absent on cereal crops on a part of the experimental farm at Samaru separated by only a few feet of grass from a field where distortion has been severe for the past six years. On the experimental farm, crop rotation is practised, dhub is weeded out, crop residues and weeds are removed and burnt and volunteer guineacorn tillers are dug up. On the field where distortion is common, guineacorn is grown every year as part of a mixed crop, the field is often not weeded or (if it is weeded) the dhub is hoed out and left lying on the ground, seedlings removed during thinning remain on the field, crop residues are seldom burnt and volunteer guineacorn is left growing to give a crop in the second year. Throughout the dry season (which extends from October to April at Samaru) mealybugs can be found on volunteer tillers of guineacorn, and it seems likely that such tillers are the main source of infestation of crops in the following growing season.

Summary.

Distortion, a severe stunting and deformation of plants of guineacorn (*Sorghum vulgare*) in Northern Nigeria, has been shown to be caused by *Heterococcus nigeriensis* Williams feeding on the plants.

The symptoms are striking; affected stems are much shorter and wider than normal and leaves are mis-shapen, with irregularly divergent veins and white tissue between the veins. Symptoms in the field vary from small patches of distortion on other normal plants to whole plants affected. The abnormal leaves of a plant with severe distortion are crumpled and remain rolled together. Growth of the plants virtually ceases if the mealybug infestation continues but, in the absence of mealybugs, affected plants recover and produce normal leaves.

Distortion has been found in the field, commonly on *Sorghum vulgare*, *Zea mays* and *Cynodon dactylon*, and once only on *Pennisetum typhoides* and *Chloris pycnothrix*, respectively, and has been produced experimentally on *Z. mays*, *C. dactylon*, *P. typhoides*, *Triticum aestivum*, *Oryza sativa* and *Digitaria exilis* by transferring mealybugs from affected guineacorn.

The mealybugs causing distortion are yellowish pink. They are found in small numbers in protected positions on affected plants and feed on meristematic tissues. A few colonies of grey mealybugs, which cannot be distinguished from the pink form on morphological grounds, were found on expanded leaves of healthy tillers; they apparently prefer to feed on mature tissues and do not normally cause distortion.

Distortion was investigated by feeding single mealybugs (after 48 hours' starvation) for limited periods on seedlings of *S. vulgare* growing in test-tubes on cotton-wool. Out of a total of 123 seedlings, 36 developed symptoms of distortion after presumed feeding times of up to 51 hr.; the shortest presumed feeding time to give rise to distortion was 7 hr. Symptoms developed rapidly, starting within 24 hr. of the commencement of feeding. After removal of the mealybugs, affected seedlings all recovered and produced healthy leaves within 11 days.

By feeding mealybugs on seedlings before the first leaf broke out of the coleoptile, it was shown that the stylets are inserted through one or more leaves to feed on the inner ones so that a single mealybug affects several leaves at one time, thus the symptoms have the appearance of being systemic.

Distortion is unlike a toxic feeding effect because it involves no wilting or death of the cells and severe symptoms can be caused by a single mealybug feeding for a short time. It resembles a simple gall the growth of which is initiated by feeding.

The main carry-over of mealybugs in the dry season seems to be on volunteer tillers of *S. vulgare*, and it is suggested that crop sanitation and improved cultural methods should give adequate control.

Acknowledgements.

I wish to thank Dr. J. M. Waterston, Director of Agricultural Research, Ibadan, for providing facilities for part of this work and Dr. T. W. Tinsley and Dr. C. H. K. Martini of W.A.C.R.I., Ibadan, and Dr. W. N. Stoner of International Co-operation Administration for valuable advice. My husband, Mr. K. M. Harris of the Department of Agricultural Research, has helped me throughout.

Reference.

- WILLIAMS, D. J. (1961). Notes on the genus *Heterococcus* Ferris (Coccoidea, Homoptera) with a description of a new species injurious to guineacorn (*Sorghum vulgare*) in Nigeria.—*Bull. ent. Res.* **51** pp. 671–675.



FIG. 1. Distortion of guineacorn, field symptoms. Plant on the right showing an early stage of distortion; healthy plant of the same age on the left.

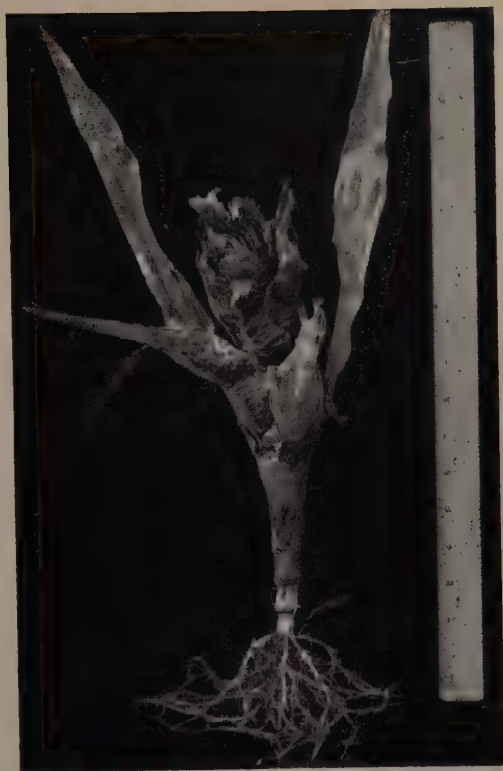


FIG. 2. Distortion of maize, field symptoms. Plant at harvest time photographed beside an 18-in. rule (healthy plants were about 6ft. high). The oldest leaves are normal.



FIG. 3. Distortion of guineacorn seedlings, experimental symptoms. Four 7-day-old seedlings, two controls on the left; photographed 6 days after single mealybugs had been placed on the two seedlings on the right (P.F.T. of 24 hr.).

THE EFFECT OF TEMPERATURE, HUMIDITY AND QUANTITY OF FOOD ON THE DEVELOPMENT AND DIAPAUSE OF *TROGODERMA PARABILE* BEAL.

By H. D. BURGESS, Ph.D.

In an extensive study of the genus *Trogoderma* (Coleoptera, DERMESTIDAE), Beal (1954) states that *T. parabile* Beal is a potentially important pest in stored commodities. Not only has *T. parabile* been found in North America on a wide range of stored food materials, but also it has a number of natural reservoirs such as the nests of birds or bees and it can feed on pollen (Beal, 1954; Strong & Okumura, 1958; Watters, 1958). Beal considers that it is not a native of North America, but will eventually be identified with a species from elsewhere. The related khapra beetle, *T. granarium* Everts, is a very serious and widespread pest of many products. To help assess the potential importance of *T. parabile*, its reproductive rate at 30°C. and 60 to 70 per cent. R.H. has been studied, together with the effect of space, temperature and humidity on larval growth. In general there is very close agreement between the present results and some very recent work by Loschiavo (1960) in Canada.

Insects and apparatus.

The experimental insects were cultured from spermatypes sent by R. S. Beal of the Arizona State University. (Spermatypes are specimens bred from the holotype and an allotype of the species.) Stock cultures were maintained at 30°C. and about 60 per cent. R.H.

Experiments were conducted over a range of temperatures and humidities. The temperatures were controlled in rooms, incubators or refrigerators to $\pm 0.5^{\circ}\text{C}$. or less. A humidity of 60 ± 3 per cent. R.H. was obtained by controlling the air in a constant-temperature room, 30 and 70 per cent. were maintained in desiccators by solutions of caustic potash (Solomon, 1951), near 0 per cent. by solid phosphorus pentoxide and 90 per cent. by a saturated solution of barium chloride (Washburn, 1926). To prevent the depletion of oxygen, the desiccators were aired as necessary, but never more frequently than once daily. To prevent the accumulation of carbon dioxide, a stick of caustic potash was included at 0 per cent. R.H. and a small dish of dilute solution at 90 per cent. R.H.

Life-cycle.

The life-cycle was studied in favourable conditions of 30°C. and 60 to 70 per cent. R.H. in order to measure the rate at which the species can increase. Individual insects were kept from the laying of the egg to the formation of the adult beetle: pairs of beetles were used to find the length of adult life and the number of eggs laid.

Development.

Newly laid eggs were obtained by leaving a group of beetles for 24 hours in a glass dish containing folds of black paper but no food or drinking water. Since the beetles can fly, the dish was covered with cotton cambric secured with elastic bands. Each piece of black paper was folded concertina-wise and loosely held together at one side with a wire paper-clip. A few eggs were laid on the bottom

of the dish and many of these were damaged by the parents: also some eggs were damaged to varying degrees when the folds of paper were dismantled, consequently no value for the natural mortality of eggs can be given.

The eggs were examined daily, and 101 of the newly hatched larvae were transferred singly on a camel-hair brush to three batches of containers, one larva to each container. Batch A consisted of 51 glass specimen-tubes (3×1 in.) each containing 15 cc. of wheatfeed; batch B comprised 20 tubes with 20 cc. of a mixture of equal parts of wheatfeed and wheat (No. 2 Manitoba); batch C consisted of 30 2-lb. jam jars each containing 450 cc. of wheatfeed. Wheatfeed consists of fine bran with a little endosperm. The mouth of each container was covered with cotton cambric, held in a tube by a cork with a hole in the centre, or over a jar by elastic bands. Near pupation time, eleven of the larvae were examined daily to obtain the dates of pupation and of the change to adult: to minimise disturbance, the rest were examined every three or four days for pupae, and the pupae were looked at daily for the change to adult.

TABLE I.

The duration of stages in the life-cycle of *T. parabile* without delayed pupation. The insects were bred singly at 30°C. and 60 to 70 per cent. R.H. with 15 to 450 cc. of food each.

Stage	No. of insects	Mean (days)	Range (days)	Remarks
Egg	378	6.4	6-8	39 larvae delayed pupation > 7 weeks: 7 others died as immature larvae: 2 larvae and 2 pupae met with accidents: all these are excluded.
Larva	51	26.1*	19-33*	
Pupa	11	4.8	4-5	
Hatching to adult ..	51	30.9	24-38	Only 11 larvae were examined daily to obtain the date of pupation. Standard error=0.40 days.
Pre-emergence ..	9	1.6	1-3	
Laying to active adult	—	38.9	31-49	Only 9 adults were examined for the emergence from the skin. Obtained by addition of the component stages.
Pre-oviposition ..	8	2.8	2-3	The other 4 males were discarded as soon as the females died. i.e., the number of days between the first and last egg.
Female adult ..	8	8.4	7-9	
Male adult ..	4	17.0	14-21	
Egg-laying	8	5.4	4-7	i.e., the day after emergence from the skin during which most eggs were laid.
Peak egg-production ..	8	3.7	3-5	
Egg laid to peak egg-production ..	—	45.4	36-57	Obtained by addition of the component stages.

* Obtained by subtracting the pupal period, which is very constant, from the time between the hatching of the egg and the formation of the adult.

Some larvae grew rapidly, apparently to maturity, and then delayed pupation for many months. The others pupated within seven weeks of hatching, and the mean durations of the developmental stages of these are given in Table I (18 insects from Group A, 12 from B and 21 from C). Since there were no significant differences between batches A, B and C, the data have been combined.

The incubation of the egg took a mean of 6 days, the larval period of insects without delayed pupation 26 days and the pupal period 5. The pupa remains covered by the last larval skin, which gapes along the dorsal split to accommodate the greater width of the pupa; the adult remained in this skin for 1 to 3 days. By combining the component stages, an over-all period from the laying of the egg to the emergence of the adult from the larval skin of 39 days is obtained. The development of the males was slightly quicker than that of the females (Table II), but unfortunately only a few of the beetles were sexed.

TABLE II.

The developmental period of males and females of *T. parabile* without delayed pupation and bred singly in 15 cc. of food at 30°C. and 60 to 70 per cent. R.H.

Sex	No. of beetles	Hatching to adult (days)		P
		Mean \pm S.E.	Range	
Female	6	30.7 \pm 0.56	29-33	0.02
Male	11	28.2 \pm 0.68	24-31	

Adult life and egg-production.

The egg-production of eight pairs of young beetles was observed. These insects were taken from stock cultures as pupae and placed individually in tubes. Within 24 hours of emerging from its pupal skin, each female adult was confined in a 2 \times 1-in. tube with a young male. Folded paper was provided, but no food or drinking water, since the adults are thought not to feed or drink. The eggs were removed and counted daily.

The female beetles lived 7 to 9 days and the males 14 to 21 (Table I). After a pre-oviposition period of 2 to 3 days, the eight females laid a mean of 67.9 eggs (standard error \pm 7.3 eggs). Of these eggs, a mean of 7.1 collapsed during the day after laying; a further 9.7 also died later, 51.1 hatching.

Of the 409 newly-hatched larvae, 300 were transferred to cultures, in which only 4 insects subsequently died as larvae or pupae. This shows a very low developmental mortality, equivalent to only 0.7 out of the mean value of 51.1 newly-hatched larvae, making the number of adult offspring produced per female parent 50.4.

It was not known for certain whether the adults would lay the same number of eggs in folds of paper without food as in a medium consisting of food. Also the mortality of eggs in the above estimate was thought to be artificially high, because without food the adults damaged some eggs and other eggs were broken by handling. An attempt to avoid such damage and to obtain the approximate number of eggs laid in food was made by allowing pairs of young adults to oviposit in large quantities of food, which were not disturbed until the offspring had grown almost to mature larvae. Eight replicate pairs were kept, each in a 2-lb. jar containing 450 cc. of wheatfeed. When the offspring began to pupate, the pupae were removed every three or four days to avoid a second generation. A mean of 56.5 offspring pupated (S.E. \pm 9.2 pupae), which is not significantly different from the estimate of 50.4 above. This suggests that similar numbers of eggs are laid in food as in folds of paper and that the number of eggs damaged in tubes without food is not important.

Rate of increase.

For the purpose of calculating the rate of increase, the mean of these two values was used (53.5 offspring per female) and all the eggs were assumed to be laid on the day of peak oviposition of the grown adult (Table I). Using the method described by Howe (1953) the rate of increase (λ) calculated for a population of stable age distribution is $\times 1.7$ per week.

TABLE III.

The effect of the volume of food on the proportion of larvae of *T. parabile* delaying pupation when kept at 30°C. and 60 to 70 per cent. R.H. from time of hatching.

Expt.	Food in each container (cc.)	Food per insect (cc.)	Percentage in first 7 weeks			No. of insects in each container	Total no. of insects
			Delayed pupation	Pupae	Lost and died		
D	450	450	6	77	17	1	30
E	450	15	5	94	1	30	180
F	140	1.4	2	98	0	100	100
G	25	2.5	20*	50*	30*	10	20
H	15-20	15-20	52	42	6	1	71
J	0.7	0.7	70	10	20	1	20

* Mean of only two cultures: four larvae delayed pupation in one and none did so in the other.

Larvae with delayed pupation.*Amount of food.*

Some of the larvae obtained from eggs at 30°C. failed to pupate. The larvae that pupated did so during the first seven weeks after hatching: the remaining

TABLE IV.

The development of larvae of *T. parabile* kept singly at 30°C., over a range of humidities in different volumes of food.

	0.7 cc. of food					15-450 cc. of food
	Near	0	30	70	90	60-70
Relative humidity (%)						
No. of newly-hatched larvae used		20	20	20	20	101
No. of large larvae with delayed pupation*		20	18	18	13	42
No. of larvae dead in first 7 weeks		0	2	0	0	6
No. of larvae pupated		0	0	2	7	53
Egg-hatching to formation of adult : mean \pm S.E. (days)	—	—	46.5 \pm 3.5	40.0 \pm 2.1		30.9 \pm 0.4
Egg-hatching to formation of adult : range (days)	—	—	43-50	38-46		24-38
P	—	—		0.2	< 0.01	

* These larvae grew to a large size in two to three months, after which they were kept at the experimental conditions for two years and then used for other experiments.

larvae grew at a similar rate for seven weeks, apparently to maturity, then stayed about the same size over periods as long as two years. In six experiments with varying numbers of larvae and different volumes of food in containers ranging in size from $2 \times \frac{1}{2}$ -in. tubes to 2-lb. jars, the proportion of larvae with delayed pupation increased with decreasing volume of food (columns 2 and 4, Table III), but was not related to the amount of food per larva (columns 3 and 4, Table III).

The degree of crowding in the cultures did not influence the delay of pupation (columns 4 and 7, Table III).

In the experiment with insects isolated in 0.7 cc. of food, the larval periods of the two insects that pupated were rather longer than those of insects kept in larger amounts of food (Table IV). This may suggest that 0.7 cc. of food is inadequate nutritionally and that possibly the larvae with grossly delayed pupation are in a state of quiescence as a result of food shortage. However, larvae with delayed pupation failed to pupate after renewal of the food, later doubling its quantity and finally giving each larva 15 cc. of food in a larger tube. In view of this it is unlikely that food shortage prevented the pupation of larvae given 0.7 cc. of food, and there is no suggestion that food shortage caused the delayed pupation of other larvae given 15 to 20 cc. of food (Table III, H).

It is possible that the heat from the body activities of larvae in the densest cultures might have increased the temperature in the middle of the food. Such an increase is not likely to exceed 1°C . Since it will be shown in the next section that the delayed pupation occurred at temperatures both above and below 30°C ., this increase is not likely to have grossly delayed pupation.

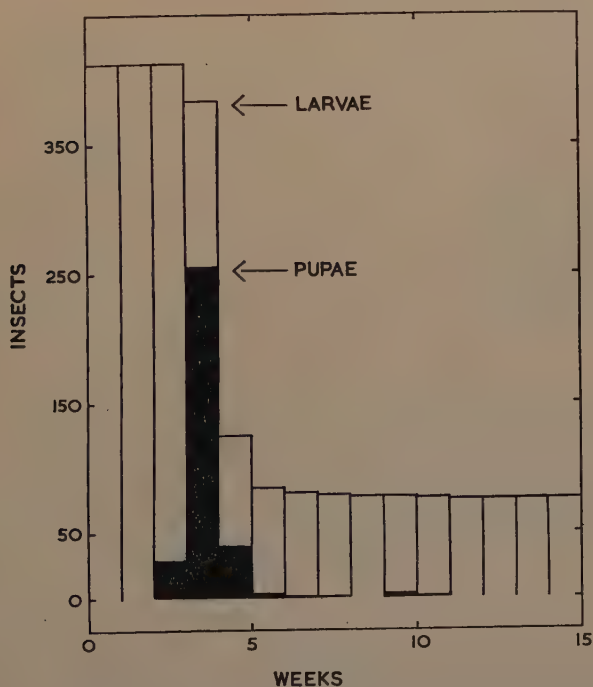


Fig. 1.—The pupation of *T. parabile* at 30°C . and 60-70 per cent. R.H. The total insects present at the end of each week are shown by the histograms, white representing larvae, and black, pupae. The pupae were removed from the cultures.

In fig. 1, the results of all the experiments in Table III have been combined, and more data have been included to cover a period of 15 weeks. All but four of the larvae that pupated did so when less than seven weeks old. This period, therefore, has been adopted arbitrarily for 30°C. and 60 to 70 per cent. R.H. as a dividing point between normal and delayed pupation.

In the first seven weeks, larvae with and without delayed pupation seemed to have similar numbers of moults and similar growth rates, but no precise record was kept of these data. Larvae that had not pupated in seven weeks continued to moult and feed occasionally. For example, one such larva, 14 weeks old, was isolated on wheat so that its faecal pellets could be sieved off daily and used as a measure of feeding (fig. 2). It fed intermittently for 10 weeks and moulted four times, then it ceased to feed for another 14 weeks, in the course of which it moulted twice more and died.

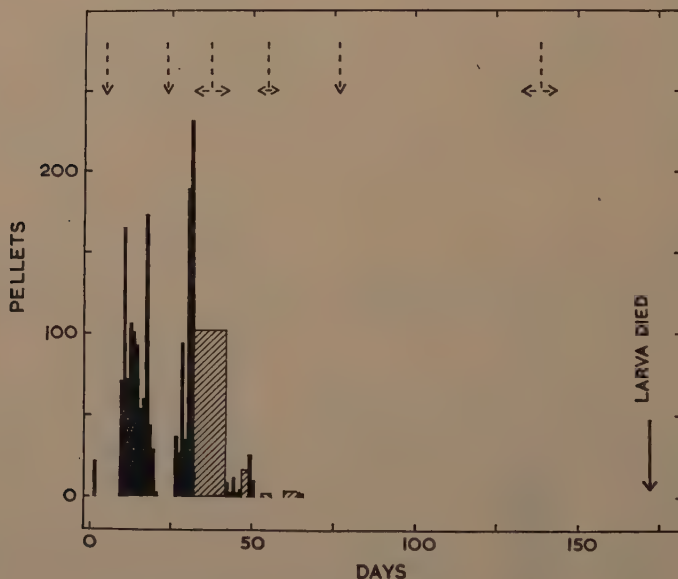


Fig. 2.—The daily production of faecal pellets by an isolated larva of *T. parabile*. Moults are shown by broken lines and the times of moulting by arrows. For three periods, during which daily observations were not made, the mean daily numbers of pellets are shown by hatched histograms and the arrows are placed horizontally. The larva was 14 weeks old when the experiment began.

Disturbance.

Loschiavo (1960) also found that many larvae failed to pupate. In addition he discovered that the daily disturbance of the food increased the number of larvae delaying pupation when bred singly in about 8 cc. of food. Therefore two batches of single larvae kept entirely undisturbed for seven weeks were compared with the batches of larvae disturbed twice weekly and sometimes daily

(Table V). Disturbance increased the proportion of larvae with delayed pupation in 15 to 20 cc. of food (using a chi-squared test, $P=0.02$), but not in 0.7 cc., in which two larvae pupated in the disturbed tubes and none in the undisturbed ones ($P<0.01$).

TABLE V.

The effect of disturbance on the proportion of larvae of *T. parabile* delaying pupation. The insects were bred singly at 30°C. and 60 to 70 per cent. R.H.

Tube	Food per tube (cc.)	Disturbance	No. of insects	Percentage in first 7 weeks		
				Lost and died	Pupae	Still larvae
3 × 1-in.	20	No	19	0	73	27
3 × 1-in.	15-20	Yes	71	6	42	52
2 × $\frac{1}{2}$ -in.	0.7	No	100	1	0	99
2 × $\frac{1}{2}$ -in.	0.7	Yes	20	20	10	70

Temperature and humidity.

At 70 per cent. R.H., 20 newly hatched larvae were reared at each temperature from 15°C. by 2.5°C. intervals to 40°C. These experiments were started before the effect of a small volume of food was discovered, and each larva was kept singly on 0.7 cc. of food. At 15 and 40°C., the larvae died in an early instar and their early death is unlikely to have been influenced by the use of only 0.7 cc. of food. At temperatures between 17.5 and 37.5°C., the larvae grew to a large size, but all except three delayed pupation, despite occasional renewal of the food and increase in quantity. Probably the small initial amount of food caused most of these larvae to delay pupation and little information about the total duration of the larval period without delayed pupation can be gleaned from this work. At 25°C., one larva became adult after 93 days; at 30°C., one did so after 43 and another after 50 days, which on average is about two weeks longer than larvae bred in large amounts of food at the same temperature (Table IV). Even though no larvae pupated, some comments can be made about the speed of larval growth to apparent maturity in 0.7 cc. of food. Growth was very slow at 17.5°C. and increased with temperature up to 35°C. The rate of growth between 27.5 and 35°C. did not vary a lot, full size being reached in five to seven weeks. The optimum temperature for rapid development is likely to be near 35°C.

Larvae were bred at 30°C. in the same manner over a range of humidities extending from near zero to 90 per cent. R.H. (Table IV). At all humidities, most of the larvae grew to a large size and then delayed pupation, probably due to the use of only 0.7 cc. of food for each larva. A few larvae pupated at the higher humidities. At 70 per cent. R.H. two larvae pupated later than those at 90 per cent. R.H. by a mean of 6.5 days, although this difference was not significant statistically, probably due to the numbers of pupae being small.

Inducement of pupation.

Attempts were made to induce pupation in 154 larvae dormant for two years by a change of temperature followed by an increase in the volume of food from 1.4 to 20 cc. (Table VI). Shortly after changing the food, larvae bred at 17.5, 20 and 22.5°C. were given an increase of 12.5°C.; those bred at 25°C. and above were placed at temperatures 15 or 17.5°C. lower for six weeks and then exposed to a temperature increase by returning them to the initial temperature. Soon after the increase in temperature and quantity of food, a quarter to a half of the

TABLE VI.

The effect of a change in temperature combined with an increase in the volume of food on ending the delay of pupation of *T. parabile* at 70 per cent. R.H.

Temperature change (°C.)	Initial no. of larvae	No. of pupae formed after the increase of temperature
17.5 to 30	10	5
20 to 32.5	16	4
22.5 to 35	10	0
25 to 10 to 25	17	5
27.5 to 10 to 27.5	15	5
30 to 15 to 30	55	0
32.5 to 17.5 to 32.5	13	0
35 to 20 to 35	10	0
37.5 to 22.5 to 37.5	8	0
Total	154	19

larvae pupated in some experiments (Table VI). The limited success of these experiments suggests that long exposure to temperatures below 20°C. followed by an increase in temperature and in the quantity of food may be worthy of further trials.

TABLE VII.

A list of foods from which *T. parabile* has been recorded* and their suitability for *T. granarium*.† *T. parabile* has been reared in the laboratory on a few foods indicated by italics.‡

Development of <i>T. granarium</i>	Cereals, grass seeds and cereal products	Whole or ground seeds of legumes and other plants	Dried fruit and other materials
Young larvae developed to adult	<i>barley, rice, rye, millet, milo, wheat, wheat germ, flour, spaghetti, oats, oatmeal, corn (or sweet corn), corn meal (or tortillas), hominy grits, breakfast and baby cereals</i>	peas, beans, soya-beans, gram (or garbanzos), alfalfa, clover, cotton, cucumber, onion, pepper, spinach, sunflower, water-melon	almond meats, walnut meats, egg noodles, yeast, pollen, milk powder, dried insects, dried beef
Young larvae died	—	—	raisins, dried peaches, dried prunes
Not tried	macaroni, rice bran, wild rice, brome, Dallis grass, fescue, rye-grass, Sudan grass, wheat grass	beet, burnet, cantaloupe, carrot, dandelion, egg-plant, lettuce, musk melon, pumpkin, safflower, sesbania, squash, tomato, vetch	beehives, candy, fudge mixes, cobwebs, mud-dauber nests, chili pepper, dehydrated chicken soup, powdered pudding, fishmeal, cookies, spider egg-masses

* Strong & Okumura (1958); Beal (1954).

† Noon (1958); Hopkins (1955); Lindgren, Vincent & Krohne (1955); Sharifi (1958); Singh & Pant (1955); Lindgren & Vincent (1959); Voelkel (1924).

‡ Strong, Okumura & Sbur (1959).

Food materials.

T. parabile has been found on a very wide range of food materials, rich in carbohydrate, protein or oil (Table VII). A number of authors have tried to breed the related species, *T. granarium*, in laboratory experiments on over half of these foods. These foods are listed in the first part of the table and young larvae of *T. granarium* developed to the adult stage on all of them except the three dried fruits.

Strong, Okumura & Sbur (1959) have bred *T. parabile* in the laboratory on a few of the foods, which are shown in italics. Since the data for *T. parabile* on other foods are records of the occurrence only of the species, and since larvae can probably survive for a long time on unsuitable foods, it seems likely that *T. parabile* may be unable to breed on many of the foods listed in Table VII. For instance, larvae of both species died or failed to become adult in 145 days at 32°C. on copra-meal, flax seed, gelatin, powdered skim-milk and raisins; *T. parabile* failed on dried brewers' yeast; some pre-cooked cereal products, *e.g.*, barley cereal and corn cereal, and some grains with the bran and the germ removed, *e.g.*, rice, were unfavourable to one or both species, probably because some essential nutritive materials had been removed in the processing; some beans were unfavourable for *T. parabile*, *e.g.*, pinto beans and lima beans (Strong, Okumura & Sbur, 1959).

Discussion.

The rate of breeding of *T. parabile* in large amounts of food under favourable conditions is comparable to that of the related serious pest, *T. granarium*. Between 60 and 70 per cent. R.H. the rate of increase (λ), calculated for a population of *T. parabile* of stable age distribution, is $\times 1.7$ per week at 30°C. Comparable values for *T. granarium* are $\times 1.5$ at 30°C. and $\times 1.8$ at 35°C. (calculated from the data of Hadaway, 1956). The very small proportion of larvae of *T. parabile* that delayed pupation has been omitted from the calculations and also it was assumed that no larvae of *T. granarium* entered diapause. Thus, when delayed pupation does not intervene, the fastest rate of breeding of *T. parabile* is probably similar to that of *T. granarium*. The two species are very similar in other respects. The temperature range of *T. parabile* (about 17 to 37°C.) is slightly below that of *T. granarium* (21 to 40°C.) and the optima are near 35 and 37°C., respectively. Moreover, *T. granarium* can breed in extremely dry conditions and larvae of *T. parabile* can develop at least to near maturity in the same conditions. Furthermore, the ranges of food materials of the two species are very similar. Consequently, in favourable conditions not inducing delayed pupation, these two pests appear to be equally likely to become serious.

In 0.7 to 20 cc. of food, the pupation of some individuals of *T. parabile* throughout the temperature and humidity range of the species is greatly delayed, even though the amount of food is more than adequate to allow the larvae to grow to their full size. The larvae can be divided into two types, those which pupate early and those which do not. Both types occur in apparently identical conditions. The frequency distribution of pupation times of the early-pupating type (fig. 1) is similar to that of many rapidly-breeding insects without delayed pupation (Burges, 1956): the mean larval period is about a month at 30°C. and 70 per cent. R.H. The other type, which does not pupate promptly, may delay pupation for more than two years and during this time individuals pupate very infrequently, even if the environmental conditions (temperature, humidity, space and food) are made favourable for growth as far as is known. It can be concluded that the larvae with delayed pupation enter a state of facultative diapause.

The extrinsic cause of the diapause appears to be the low total volume of food available to the larva. The effective factor may be either the volume of food

material into which the larva may tunnel or else the surface area of the mass of food material. Disturbance may increase the numbers of larvae entering diapause. In large volumes of food, the degree of crowding or the amount of food available per larva, within the limits tested, appears to have no effect. This suggests that the accumulation of faecal pellets in the food also has no effect.

This diapause has both similarities to and differences from that of *T. granarium*. The similarities include the occasional moulting and feeding during diapause and the ability to walk about if disturbed. The main differences are the cause and strength of diapause. The diapause of *T. parabile* is induced by keeping the larvae in small amounts of food, irrespective of the degree of crowding and the accumulation of faecal pellets. That of *T. granarium* is due to low temperature combined with the accumulation of faecal pellets in the food, and it is therefore influenced by crowding. The diapause of *T. parabile* is more strongly developed than that of *T. granarium*, because it can occur in most individuals throughout the temperature range, whereas in *T. granarium* it has occurred less frequently at high temperatures than at low ones (Burges, 1956); also, changes in temperature and food, which have little effect on the diapause larvae of *T. parabile*, will break the diapause of many larvae of *T. granarium* (Burges, 1956, 1959).

The determination of diapause by the volume of food is unusual. No similar instance has been found in the literature. It appears that in a small quantity of food, the intervention of diapause would reduce the rate of breeding before all the food was eaten. Presumably, in food stores, limited breeding would take place in small residues of food, and rapid breeding would proceed in large bulks. In mills, the amount of breeding would possibly be controlled by the size of the static accumulations of food in the machinery. A similar control can be imagined in the natural habitats of the species.

More information about the diapause is required before a firm opinion can be given about the effect of the diapause on breeding in food stores. Specimens of *T. parabile*, which found their way into some bulks of cereals experimentally inoculated with *T. granarium*, bred much less than *T. granarium*: *T. parabile* became very scarce after moderate numbers of *T. granarium* appeared (W. L. Nutting, University of Arizona, personal communications). This may indicate that the diapause of *T. parabile* inhibited breeding more than did that of *T. granarium*. However, in view of the different causes of diapause, the amount of inhibition in the two species would be expected to vary in different circumstances.

Summary.

The rate of development and the egg-production of the Dermestid beetle, *Trogoderma parabile* Beal, at 30°C. and 60 to 70 per cent. R.H. and the effect upon larval development of the volume of food, the temperature and the relative humidity have been determined.

In 15 to 450 cc. of wheatfeed at 30°C. and 60 to 70 per cent. R.H., active adults are formed from eggs in a mean of 39 days (egg 6, larva 26, pupa 5 and pre-emergence 2). Males develop slightly more rapidly than females. On average, a female adult lives 8 days and 53 of her offspring reach maturity. The weekly rate of increase of a population of stable age distribution (λ) is $\times 1.7$.

At temperatures between 17.5 and 37.5°C. (and at 70 per cent. R.H.) and at humidities between near 0 and 90 per cent. R.H. (and 30°C.) larvae can grow to a large size; but in 0.7 to 25 cc. of food some of these large larvae enter a facultative diapause, as a result of restricted space. Disturbance of the food increases the proportion of diapause larvae. The diapause larvae feed and moult intermittently. At 30°C. and 60–70 per cent. R.H., a period of seven weeks after hatching has been adopted arbitrarily to distinguish diapause and non-diapause larvae. Only a limited success was obtained in breaking the diapause, which is less readily broken than that of *T. granarium* Everts.

Without diapause, the two species breed at a similar rate. They have similar, wide ranges of humidity and food material. The temperature range of *T. parabile* is probably a little below that of *T. granarium*, but equally wide. It is considered that *T. parabile* may become an important pest, but less serious than *T. granarium*.

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References.

- 64 262 BEAL jr., R. S. (1954). Biology and taxonomy of the Nearctic species of *Trogoderma* (Coleoptera: Dermestidae).—*Univ. Calif. Publ. Ent.* **10** pp. 35–102.
- BURGES, H. D. (1956). The biology and behaviour of *Trogoderma granarium* Everts.—Ph.D. thesis, Univ. London.
- 815 BURGES, H. D. (1959). Studies on the Dermestid beetle *Trogoderma granarium* Everts. III. Ecology in malt stores.—*Ann. appl. Biol.* **47** pp. 445–462.
- HADAWAY, A. B. (1956). The biology of the Dermestid beetles, *Trogoderma granarium* Everts and *Trogoderma versicolor* (Creutz.).—*Bull. ent. Res.* **46** pp. 781–796.
- HOPKINS, L. (1955). Food preferences of the khapra beetle.—*J. econ. Ent.* **48** pp. 332–333.
- HOWE, R. W. (1953). The rapid determination of the intrinsic rate of increase of an insect population.—*Ann. appl. Biol.* **40** pp. 134–151.
- LINDGREN, D. L. & VINCENT, L. E. (1959). Biology and control of *Trogoderma granarium* Everts.—*J. econ. Ent.* **52** pp. 312–319.
- LINDGREN, D. L., VINCENT, L. E. & KROHNE, H. E. (1955). The khapra beetle, *Trogoderma granarium* Everts.—*Hilgardia* **24** pp. 1–36.
- LOSCHIAVO, S. R. (1960). Life-history and behaviour of *Trogoderma parabile* Beal (Coleoptera: Dermestidae).—*Canad. Ent.* **92** pp. 611–618.
- NOON jr., Z. B. (1958). Food habits of the khapra beetle larva.—*J. econ. Ent.* **51** pp. 465–467.
- SHARIFI, S. (1958). Contributions to the biology of *Trogoderma granarium*.—*Rep. Govt Pest Infest. Lab. Denm. 1955–56* pp. 64–68.
- SINGH, K. R. P. & PANT, N. C. (1955). Nutritional studies on *Trogoderma granarium* Everts. Effects of various natural foods on the development.—*J. zool. Soc. India* **7** pp. 155–162.
- SOLOMON, M. E. (1951). Control of humidity with potassium hydroxide, sulphuric acid, or other solutions.—*Bull. ent. Res.* **42** pp. 543–554.
- 410 70. STRONG, R. G. & OKUMURA, G. T. (1958). Insects and mites associated with stored foods and seeds in California.—*Bull. Calif. Dep. Agric.* **47** pp. 233–249.

- 41 22 STRONG, R. G., OKUMURA, G. T. & SBUR, D. E. (1959). Distribution and host range of eight species of *Trogoderma* in California.—*J. econ. Ent.* **52** pp. 830–836.
- VOELKEL, H. (1924). Zur Biologie und Bekämpfung des Khaprakäfers, *Trogoderma granarium* Everts.—*Arb. biol. Reichanst., Berl.* **13** pp. 129–171.
- WASHBURN, E. W. Ed. (1926). International critical tables. Vol. III.—444 pp. London, McGraw Hill.
- WATERS, F. L. (1958). Meeting the insect problem in flour mills.—*Canad. Grain J.* **14** repr. 2 pp.
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THE DIURNAL FEEDING ACTIVITY OF *GLOSSINA PALLIDIPIPES* AUST. IN RELATION TO TRYPANOSOME CHALLENGE.

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In tsetse and trypanosomiasis control we are confronted with two major investigational problems: that of measuring the efficacy of reclamation schemes as reflected by changes in tsetse density, and that of the estimation of trypanosome challenge which has been defined (Smith & Rennison, 1960) as the number of infected bites from tsetse flies which a host receives in unit time. 48 151
47 41

The importance of challenge as a measure of the degree of danger of *Glossina* to cattle has been recognised by various workers (Anon., 1955; Rennison, 1958) and it has been suggested by Whiteside (in Smith & Rennison, 1960) that its index be defined as the product of the apparent density (*i.e.*, the number of non-teneral flies * per 10,000 yd.) and the infection rate. Further consideration of the various factors involved in challenge (Smith & Rennison, 1960) has shown, however, that this index is far from valid, and a new approach to the problem is required.

In the writers' opinion, particular stress should be laid on the methods to be employed in obtaining the sample of tsetse on which challenge is to be based. Numerous methods of sampling tsetse populations have been used in the past. These include fly-rounds (Ford & others, 1959) bait-ox rounds (Vanderplank, 1944), traps (Morris & Morris, 1949; Smith & Rennison, 1958), motor vehicles (Jack, 1941) and bicycle patrols with sticky screens.

In one form or another all the methods have their merits, but the use of apparent density (A.D.), calculated from these methods, as a factor in the determination of challenge is limited for a number of reasons. In the first place, A.D. is normally an expression of the number of non-teneral male flies caught per 10,000 yd.: thus it takes no account of the female element of the population. However, even if we include female flies caught on a fly round or line transect, as Whiteside (in Smith & Rennison, 1960) has done, we are still not dealing with the feeding population, since a high proportion of tsetse caught on a fly-round are not hungry and do not attempt to feed.

A.D. is rather a measure of undefined activity in relation to a variety of attractants, *viz.*, humans, screens, bait-animals, or any others employed. It does not refer specifically to feeding activity in relation to a given host. Moreover it is known that the activity of tsetse varies diurnally (Vanderplank, 1948; Moggridge, 1949; Williams, 1943; Fiske, 1920; Van den Berghe, Lambrecht & Christiaensen, 1956; Nash, 1937), and A.D. is calculated from the activity of tsetse flies over a limited period of the day only. It tells us nothing about activity over any other period of the day. In the estimation of challenge it would therefore seem essential to take account of diurnal feeding activity.

The disadvantages associated with the use of A.D. in determining challenge are fully realised by most workers. Smith & Rennison (1958) have investigated the use of traps as a sampling method, comparing the diurnal activity of *G. pallidipes* Aust., in relation to these, with that in relation to short-horned East

* Apparent density has long been defined as the number of non-teneral male flies per 10,000 yd., but Whiteside, in his present use of the term, includes non-teneral females. 48 152
48 151

African Zebu bullocks. The results showed that the number and pattern of the catch off the cattle was very different from the number and pattern of the catch from traps. Although these catches may, in some way, be related, it would appear desirable to use specified host-animals in the estimation of challenge, since the proportion of those flies attracted to traps that represents the feeding element of the population is uncertain.

Any estimate of challenge, then, based on (a) a feeding portion of the population, (b) activity in relation to a given host, (c) total period of tsetse feeding activity (or parts thereof) as the unit of time, (d) the infection rate, would seem to eliminate some of the disadvantages associated with previous methods of estimation.

The work now to be described was undertaken with these points in mind and with the object of finding out what pattern of diurnal feeding activity would be presented by *G. pallidipes* in the late dry season.

Description of the area in which the work was undertaken.

The experiment was conducted from the tsetse research station at Rekomitjie in the Zambezi Valley, Southern Rhodesia (16°10'S., 29°25'E., altitude 1,673 ft.) during the months of October and November 1959. The site chosen was within walking distance of the camp and consisted of a band of fairly dense vegetation flanked on both sides by less dense vegetation.

Vegetation.

Top-storey species composition (all in leaf during the experiment).—*Acacia albida* (70 ft.), *Tamarindus indica* (45 ft.), *Kigelia pinnata* (50 ft.), *Lonchocarpus capassa* (40 ft.), *Cordyla africana* (70 ft.).

Under-storey species composition (leafless during the experiment).—*Grewia* spp., *Diospyros* sp., *Popowia obovata*, *Allophyllus* sp., *Lecaniodiscus fraxinifolius*, *Capparis* sp., *Strychnos* sp., some not identified.

Climbers.—*Combretum* sp., *Strophanthus* sp., one not identified.

Ground flora.—Nothing was growing, or appeared to have grown, in the deep layer of raw humus beneath the larger trees, and the surrounding grassland had all been burnt just before the start of the experiment.

Game.

In spite of the proximity of the camp to the experimental site, certain species of game animals appeared to be resident in the area, and tsetse flies were plentiful. In the event of the presence of the workers disturbing the game it was hoped that the tsetse population could be maintained on the ox. In fact, kudu, duiker, grysbok and baboons were seen during the period of the experiment; elephants passed through the area regularly on their way to and from water, and the spoor of bushbuck and impala were also noted.

Method.

A black ox was tethered beneath a large example of *Acacia albida* from before dawn until after dusk, being moved only for a short time during the midday period into the shade of *Tamarindus indica*, 10 yd. away, when there was little shade beneath the *Acacia*. Hay and water were provided for the ox throughout the experiment.

To ensure that the sample of tsetse represented only the feeding population, all flies were allowed to engorge on the ox before being caught.

The sex of each fly and the time of catching, to the nearest five minutes throughout the period (0445-1845 hr.) during which observations were made, were recorded, and each fly marked on the 25,000 marking system (Jackson, 1953) before release. During the evening period, after sundown (mean time 1820 hr.), a Tilley lamp suspended in a tree 15 yd. from the ox was necessary for marking, and beam torches were used to locate flies on the ox.

Psychrometer readings were taken every quarter of an hour (later, every half hour) and, when more equipment was received, barometric pressure and light readings (using a Weston photographic meter) were made every half hour.

All data were recorded by the writers, the catching and marking being carried out by African field staff.

Results and discussion.

Feeding activity.

The pattern of diurnal feeding activity obtained from the experiment is shown in fig. 1.

Examination of the data reveals a slight excess of female over male flies (mean female percentage was 59.2). The over-all pattern of activity of the two sexes is, however, similar, and most striking.

There are two peak periods of activity, a small one rising rapidly from 0515 to 0545 hr. and falling slowly to 0715 hr., and a large one rising rapidly from 1545 hr., reaching a peak at 1815 hr., and dropping suddenly to nothing by 1845 hr. During this evening peak, the legs of the ox became covered with an almost solid mass of feeding and probing individuals of *G. pallidipes*.

This pattern of activity shows a strong resemblance to that found by Vanderplank (1948), a graph of which is published in Buxton (1955). The difference in activity between male and female flies was, however, much more marked than in the present experiment.

The pattern of diurnal activity of *G. pallidipes* in the dry season obtained by Moggridge (1949) working at Kilifi, Kenya, makes an interesting comparison, since he found the activity to be very much greater during the morning period than in the evening. Similarly, Williams (1943), working in Portuguese East Africa in October, found the morning peak to be greater than the evening one.

Climatic factors.

Comparison of the mean number of fed flies during five days, taken per half-hour, with mean readings of temperature, humidity, barometric pressure and light intensity, suggested no clear relationship between feeding activity of *G. pallidipes* and these factors. The data obtained, however, represent only the conditions prevailing during the late dry season and further work at other times of the year may give some indications of the factors that limit diurnal activity in the field.

The attractiveness of hide colour of host and light intensity thereon as factors affecting feeding site.

Recently, Barrass (1960), also working at Rekomitjie, has made comparative studies on black, grey and white screens as attractants to tsetse. He noted in the case of *G. morsitans* Westw., that more flies are attracted to a dark surface on which sunlight is falling directly, than to a dark surface in the shade. In the present experiment we were able to test whether individuals of *G. pallidipes* that are feeding react in this way.

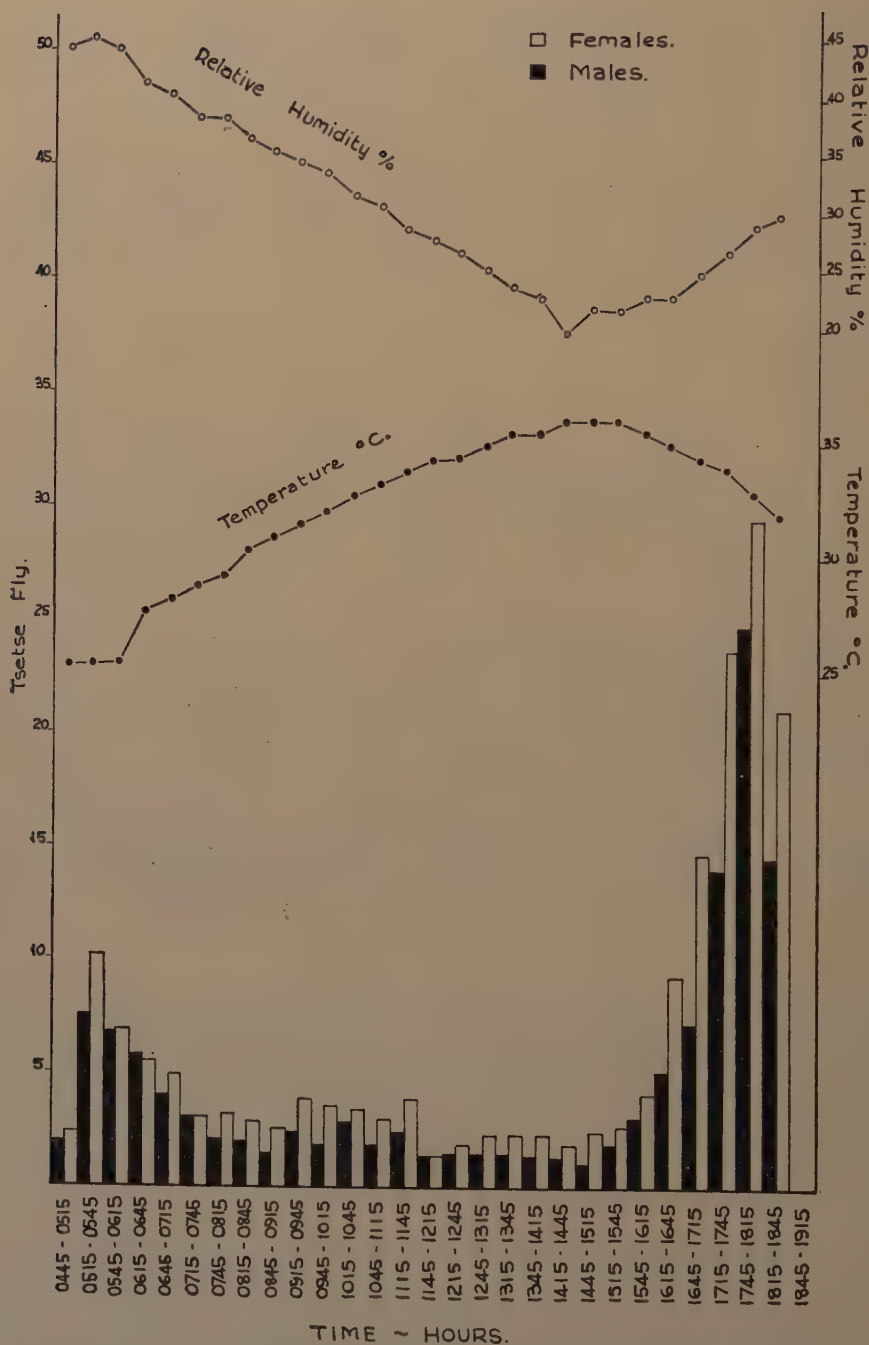


Fig. 1.—Pattern of diurnal feeding activity of *G. pallidipes*. Mean number of fed flies, male and female, taken per half-hour, on 15 separate, though not consecutive, days between 21.x.59 and 30.xi.59.

From 0530 to 1000 hr., the sun was shining directly on to one side (east) of the black ox off which the flies were caught. Analysis of the records (Table I) shows that significantly more flies were taken off the west side than the east, *i.e.*, more flies fed on the shaded side of the ox. From 1330 to 1800 hr., the ox was standing in the shade of a specimen of *Tamarindus indica* and again significantly more flies were taken off the west side, although that side was then if anything slightly the brighter. These results indicate that the difference in the catches was not due to the presence or absence of sunlight on the hide of the ox. The vegetation on the east side was open and that on the west fairly dense, and this difference may provide an explanation of the observations.

TABLE I.

Catches of *G. pallidipes* (fed flies) from different sides of a bait-ox, November 1959.

Date			0530-1000 hr.		1330-1800 hr.	
			East	West	East	West
November	4	..	6	13	59	104
"	6	..	21	40	36	58
"	7	..	14	15	29	48
"	9	..	42	53	47	59
"	13	..	64	88	63	77
"	15	..	36	38	29	39
"	24	..	0	5	45	45
"	25	..	8	12	25	36
"	27	..	16	34	28	24
"	30	..	23	27	7	24
Total	230	325	368	514

Further work on the relative attractiveness of various colours of the hide of oxen to tsetse would be of value. It was noted, during the present experiment, that fewer flies were taken off a red ox than off a black ox standing some ten yards away, the numbers, over one day's catch, being 95 and 249, respectively. There are indications, however, which the writers intend to follow up, that the red ox on its own would attract the same feeding population as the black ox. D. F. Lovemore (unpublished), also working with *G. pallidipes* in the Zambezi Valley, was unable to demonstrate any significant difference between the numbers of tsetse flies taken off a black and a red ox working a bait-ox round in company.

Estimation of challenge.

Consideration must now be given to the kind of challenge that can be estimated from the factors investigated in the experiment. The following information on feeding-population density and trypanosome infection rate was obtained:—

- The mean number of non-teneral flies that fed on a black ox per day (0445-1845 hr.) was 289. A fly was judged to have been teneral before it fed if the thorax was soft. Flies that have never taken a blood meal (*i.e.*, teneral flies, of which the mean number taken per day was only 14) cannot, of course, be infected.
- The infection rate in 613 non-teneral flies caught in the immediate vicinity of the experiment during October and November 1959 was 9.8 per cent.

From this the challenge may be expressed as the mean number of infected flies which fed on one ox in one day, which was 28.32. Alternatively, the index may be expressed as the number of infected flies per hour that fed on the ox for any specified part of the day (see Table II). This has the advantage of showing how considerably the challenge may vary within the day. Thus, in the late dry season, the danger from *G. pallidipes* is greater in the early morning than at midday and is particularly great at dusk. Under these circumstances, the normal practice of grazing cattle in the early morning and watering them in the late evening tends to increase the chance of infection. Further investigation of the diurnal feeding activity of species of *Glossina* might suggest improvements in livestock management designed to decrease the incidence of infection.

TABLE II.

Diurnal variation in challenge by *G. pallidipes*.

Time	Total non-teneral flies	Infected flies	Infected flies per hour
0445-0945	83	8.13	1.63
0945-1415	39	3.82	0.85
1415-1845	167	16.37	3.64
0445-1845	289	28.32	2.02

Infection rate assumed to be 9.8 per cent. (see p. 701, (b)).

The figures obtained for challenge to a particular ox in the present experiment are based on the feeding element of a tsetse population at a given place during a particular season, and thus appear to give a more valid estimation of challenge than has hitherto been put forward. Any simple expansion of this experiment, incorporating a measure of the time taken for a given number of hosts to become infected in the presence, or absence, of drugs, together with additional information on the species of trypanosomes involved in the infection rate, would be of value in planning drug regimes.

Observations on the feeding population.

On examination of the results of the experiment that have a bearing on challenge, it is clear that certain factors have not been taken into consideration and these may vitiate the use of this type of information. Let us examine some of the observations made on the feeding element of a population of *G. pallidipes* in this light.

(a) During the evening attack, the ox suffered considerable stress and attempted to dislodge the flies by swishing the tail, swinging the head across the forelegs and even kicking and shaking the legs. Considerable numbers were seen to be brushed off, of which some were killed, but others alighted again to continue feeding. Moreover, the field assistants' attempts to catch engorged flies that were closely surrounded by probing or half-fed flies caused temporary dispersal of the latter, which very soon settled again. The problem of how to make allowance for this phenomenon of multiple probing in areas of high tsetse density seems almost insoluble.

(b) During the evening peak period of activity, the high density of flies made it impossible to catch all the engorged ones, so that the number recorded is an underestimate. This inaccuracy would not occur at a lower tsetse density.

(c) A third factor in the determination of challenge, to which attention has been drawn by Smith & Rennison (1960), is that of the hunger cycle of tsetse flies. While we agree that this must certainly affect the challenge, it seems unnecessary to introduce any measure of the hunger of the tsetse population. If a short hunger-cycle increases the proportion of the population that will feed over a given period, this must be reflected in the number of flies caught off the host. Similarly, if a short hunger-cycle tends to increase the chances of a fly becoming infected, this will be reflected in the measure of the infection rate.

It is assumed that the infection rate remains constant throughout the day.

It is concluded that the information obtained from the type of work here described is more valid in the estimation of challenge than the information obtained by the use of traps or A.D. as calculated from any type of fly round.

[R.A.E. 2 48151 of 020 42152]

Summary.

The limitations of the use of apparent density in estimating trypanosome challenge are discussed, and it is concluded that such estimates should be based on the feeding portion of the tsetse population, its activity in relation to a given host, the total period of feeding activity (or parts thereof) as the unit of time, and the trypanosome infection rate. [247 417]

A method of investigating the diurnal feeding activity of *Glossina pallidipes* Aust. in the late dry season at Rekomitjie, in the Zambezi Valley in Southern Rhodesia, is described. A black ox was tethered daily under a large tree from before dawn until after dusk. Only flies that engorged on the ox were caught; the time of capture and sex of each fly was recorded, and the fly then marked and released. Catches were made on 15 separate but not consecutive days between 21 October and 30 November, 1959.

Diurnal activity extended from 0445 to 1845 hr., there being a small early-morning peak, reduced activity over the midday period, and a comparatively large evening peak. Climatic factors were recorded but no conclusions could be drawn about their separate effects on activity.

The infection rate of 613 non-teneral flies caught over the same period in the immediate vicinity of the experimental site was 9.8 per cent., and the mean number of non-teneral flies that fed on the ox per day (0445–1845 hr.) was 289. Trypanosome challenge, calculated as the mean number of infected flies that fed per hour, was thus 2.02 over the whole day, but varied from 0.85 during the middle of the day (0945 to 1415 hr.) to 1.63 in the early morning (0445 to 0945 hr.) and 3.64 during the latter part of the day (1415 to 1845 hr.).

Under these circumstances, the normal practice of grazing cattle in the early morning and watering them in the late evening would tend to increase the chance of infection.

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References.

- ANON. (1955). Department of Veterinary Services (Kenya). Annual report 1954.—107 pp. Nairobi.
- BARRASS, R. (1960). The settling of tsetse flies *Glossina morsitans* Westwood (Diptera, Muscidae) on cloth screens.—*Ent. exp. appl.* **3** pp. 59–67.
- BUXTON, P. A. (1955). The natural history of tsetse flies.—*Mem. Lond. Sch. Hyg. trop. Med.* no. 10, 816 pp. London, Lewis.

- FISKE, W. F. (1920). Investigations into the bionomics of *Glossina palpalis*.—*Bull. ent. Res.* **10** pp. 347–463.
- FORD, J., GLASGOW, J. P., JOHNS, D. L. & WELCH, J. R. (1959). Transect fly-rounds in field studies of *Glossina*.—*Bull. ent. Res.* **50** pp. 275–285.
- JACK, R. W. (1941). Further studies in the physiology and behaviour of *Glossina morsitans* Westw.—*Mem. Dep. Agric. S. Rhod.* no. 3, 54 pp.
- JACKSON, C. H. N. (1953). A mixed population of *Glossina morsitans* and *G. swynnertoni*.—*J. Anim. Ecol.* **22** pp. 78–86.
- MOGGRIDGE, J. Y. (1949). Climate and the activity of the Kenya coastal *Glossina*.—*Bull. ent. Res.* **40** pp. 307–321.
- MORRIS, K. R. S. & MORRIS, M. G. (1949). The use of traps against tsetse in West Africa.—*Bull. ent. Res.* **39** pp. 491–528.
- NASH, T. A. M. (1937). A statistical analysis of the climatic factors influencing the density of tsetse flies, *Glossina morsitans* Westw.—*J. Anim. Ecol.* **2** pp. 197–203.
- RENNISON, B. D. (1958). Taux d'infection des mouches tsé-tsés et estimation du nombre de trypanosomes nécessaires à l'infection.—*6th Mtg int. sci. Comm. Tryp. Res., Salisbury 1956* pp. 51–60.
- SMITH, I. M. & RENNISON, B. D. (1958). Studies on sampling methods for *Glossina* populations.—*Rep. E. Afr. Tryp. Res. Org. 1956–57* pp. 43–46.
- SMITH, I. M. & RENNISON, B. D. [1960]. Some factors concerned in trypanosome challenge.—*7th Mtg int. sci. Comm. Tryp. Res., Brussels 1958* pp. 63–66.
- VAN DEN BERGHE (L.), LAMBRECHT, F. L. & CHRISTIAENSEN, A. R. (1956). Étude biologique et écologique des glossines dans la région du Mutara (Ruanda).—*Mem. Acad. R. Sci. colon., Cl. Sci. nat.* 8° (N.S.) **4** fasc. 2, 103 pp.
- VANDERPLANK, F. L. (1944). Studies of the behaviour of the tsetse-fly, *Glossina pallidipes*, in the field: the attractiveness of various baits.—*J. Anim. Ecol.* **13** pp. 39–48.
- VANDERPLANK, F. L. (1948). Studies of the behaviour of the tsetse-fly (*Glossina pallidipes*) in the field: influence of climatic factors on activity.—*J. Anim. Ecol.* **17** pp. 245–260.
- WILLIAMS, W. L. (1943). On the activity of the tsetse, *Glossina pallidipes* and other tsetse during a 24 hour period.—*Rhod. agric. J.* **40** pp. 368–370.

SEASONAL VARIATIONS IN THE FAT CONTENT AND SIZE OF *GLOSSINA SWYNNERTONI* AUSTEN.

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Some years ago, the late Dr. C. H. N. Jackson described seasonal variations in mean size of *Glossina pallidipes* Aust., *G. morsitans* Westw. and *G. swynnertoni* Aust. (Jackson, 1953). In the case of *G. swynnertoni* the publication was evidently intended as an interim report, for Dr. Jackson continued the work, which included unpublished data on fat content, after the appearance of the first paper. The observations were carried on after the death of Dr. Jackson in 1955, and in the present communication the full results of this long-term investigation (1945-1958) are considered.

Material and methods.

The males of *G. swynnertoni*, on which this investigation is based, were collected on standard fly-rounds (see Buxton, 1955) in an area of untouched bush near Shinyanga, Tanganyika. For a description of the area (Block 9) see Harrison (1936). Early samples were about 100 (exact figures given in Jackson, 1953); after 1948 the monthly sample was 30-60 until June 1953, when it was standardised at 30 per month. From each fly, one wing was removed and mounted dry. The length of the middle part of the fourth longitudinal wing vein was used as an estimate of size (Jackson, 1946) and the monthly mean values for non-teneral males are given in Table I. The flies were dried in bulk to constant weight at 75°C., the weight of the detached wing being ignored, after which chloroform-soluble substances (referred to as fat) were extracted in several changes of solvent, to constant weight of the subsequently dried flies. Fat content exhibited a marked annual cycle (Table II), in other words, as had long been suspected, the tsetse population is better fed at some seasons than at others. Not all the observed variation, however, could be attributed to changes in nutritional status, since in the first place the fat content of flies, other things being equal, had been found to be strongly correlated with size (unpublished observation), so that differences in mean size between samples would necessarily be associated with corresponding differences in fat content. Secondly, it is well known that the fat content of flies is different from one hunger stage to the next (*e.g.*, Jackson, 1933), and, since the proportion of the different hunger stages caught varies within wide limits from day to day, this will constitute another source of variation.

Collections of *G. swynnertoni* made by one of us (E.B.) during July 1958 and February 1959 have enabled fairly accurate estimates to be made of the relation between fat content and size. The regressions are not constant throughout the year, but for present purposes it was considered legitimate to adopt a mean value corresponding to a difference of 0.117 mg. fat for every 0.01 mm. difference in vein length. Using this relation, the fat contents of samples of the present collection have been corrected to 1.430 mm. vein length, near the mean for the series as a whole. In this way the contributions made by random and seasonal fluctuations in size to the variance of the fat have been in some measure removed.

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TABLE I.

The mean vein length of samples of non-teneral males of *G. swynnertoni* collected in Block 9, Shinyanga.

	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958
January ..	—	1.425	1.437	1.405	1.433	1.432	—	1.440	1.440	1.422	1.424	1.421	—	1.406
February ..	—	1.443	1.459	1.452	—	1.438	—	1.466	—	1.433	1.424	1.432	1.442	1.423
March ..	—	1.450	1.445	1.429	1.431	1.443	—	—	1.436	1.451	1.458	1.432	1.445	1.443
April ..	—	1.417	1.448	1.440	1.429	1.444	1.435	1.428	1.434	1.433	1.438	1.434	1.425	1.401
May ..	—	1.424	1.442	1.445	1.433	1.439	1.431	1.436	—	1.446	1.430	1.442	1.447	1.409
June ..	1.438	1.443	—	1.442	1.434	1.430	1.465	—	1.449	1.446	1.413	1.426	1.427	1.393
July ..	—	1.443	1.435	1.454	1.459	1.429	1.465	1.446	1.458	1.436	—	1.440	1.440	1.432
August ..	—	1.438	1.435	1.430	1.425	1.429	1.418	1.446	1.420	1.435	1.431	1.397	1.415	1.390
September ..	1.434	1.420	1.437	1.428	1.430	1.438	1.429	—	—	1.402	1.422	1.412	—	1.408
October ..	1.419	1.426	1.432	1.442	1.411	1.439	1.419	—	1.427	1.429	—	—	1.401	1.414
November ..	1.411	1.419	1.420	1.423	1.445	1.420	1.441	—	1.417	1.394	1.410	1.395	1.407	1.400
December ..	1.418	1.428	1.431	1.439	1.430	1.450	1.435	—	1.408	1.391	1.409	1.408	1.399	1.412

TABLE II.

Fat content in milligrammes of samples of non-teneral males of *G. swynnertoni*.

	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	Mean
January ..	—	1.63	2.80	2.77	2.17	2.25	—	2.60	2.48	1.63	2.87	2.98	—	2.60	2.43 ± .14
February ..	—	2.34	2.24	2.57	—	—	—	2.17	—	1.87	2.79	1.87	2.56	2.05	2.28 ± .11
March ..	—	2.40	1.87	2.43	2.31	2.67	—	3.04	2.72	2.27	3.16	2.35	2.82	1.49	2.46 ± .14
April ..	—	2.67	2.10	1.81	2.26	2.39	—	4.34	2.58	2.37	2.54	2.05	3.49	2.43	2.59 ± .20
May ..	—	2.16	1.84	2.58	2.76	2.40	—	2.56	—	2.41	2.51	2.20	3.73	—	2.515 ± .16
June ..	2.20	1.87	—	2.32	2.17	1.70	—	—	2.59	2.64	2.64	1.96	1.69	2.07	2.16 ± .10
July ..	—	1.91	2.19	2.48	2.17	2.16	—	1.86	—	1.90	—	2.57	1.57	2.63	2.144 ± .11
August ..	—	2.17	2.16	2.17	1.92	2.20	—	—	—	1.92	2.19	2.45	1.43	2.19	2.08 ± .09
September ..	—	1.96	2.25	1.69	1.95	2.16	—	—	—	1.76	1.80	1.65	—	2.16	1.88 ± .09
October ..	1.98	1.66	2.18	1.88	1.95	2.36	2.51	—	1.34	1.97	—	2.27	1.77	2.27	2.01 ± .10
November ..	2.00	2.40	2.08	2.36	3.00	2.50	2.44	—	2.23	2.04	2.15	2.35	1.86	1.80	2.25 ± .09
December ..	2.03	2.49	2.32	2.68	2.66	2.62	2.50	—	1.66	2.32	2.17	3.07	2.58	2.76	2.45 ± .10

The figures in this Table have not been corrected for size of fly.

An attempt to account for the variation in fat content associated with differences in the mean hunger stages of the samples collected was made in the following way: flies collected in the field were starved to death at high humidities (to exclude death by desiccation) and the relation established between wing-vein length and the residual (non-fatty) dry weight of the starved fly. Knowing the mean wing-vein length of a given sample, a rough estimate could now be made of the quantity of undigested blood in the gut, by subtracting the non-fatty dry weight of starved flies of that size from the observed non-fatty dry weight. This residual blood-meal was then expressed as a percentage of the full meal * which a fly of that size would take, to give the percentage residual blood-meal (RBM%). When the mean fat contents of samples were plotted against the mean RBM percentage a correlation was obtained, the value of the regression coefficient being 0.02673 ± 0.0058 . With this value it was now possible to correct the mean fat content of individual samples to a standard level of RBM percentage; the modal value of 12.9 was chosen, corresponding approximately to a stage-III fly in the notation of Jackson (1933).

The estimates to be discussed below thus represent what the fat content of flies would have been had there been no difference between samples in respect of mean size, and had the samples all been drawn from flies at the same stage of digestion. The corrections considerably reduced the annual variation, and reduced the variance in any one month by some 11 per cent.

Meteorological observations were made at the Research Laboratory about two miles south of the collecting area, and included records of the rainfall, the mean temperature (taken as the mean of the maximum and minimum), the saturation deficit at 2 p.m. and the hours of sunshine.

Results.

Seasonal changes in the mean size of G. swynnertoni.

Seasonal variations in the mean size of tsetse flies at Shinyanga may be taken as representing roughly corresponding variations in the conditions to which the pregnant females were exposed two months previously (allowing 35 days for pupal development and a mean male age of about 4 weeks (Jackson, 1953)). The mean temperature during 13 years of observation was never above 26.7 or below 21.2°C., and assuming that the temperature of pupal sites is not greatly different (as concluded by Jackson (1946) in the same place) the direct effect of developmental temperature on size (Bursell, 1960) may be ignored. The full data are presented in Table I. The mean values for each of the 12 months are shown in fig. 1, and in calculating these the very incomplete years 1945, 1951 and 1952 have been omitted. Broadly speaking it may be said that flies tend to be small from August to January (mean 1.421 mm.) and large from February to July (mean 1.436 mm.); this apparently trivial difference of 1 per cent. in wing vein length in fact represents a difference of 5 per cent. in the live weight of flies. There appears to be a less well-defined decrease in size during April, May and June.

Seasonal changes in the fat content of G. swynnertoni.

The mean monthly fat content of non-teneral males, corrected as explained above to a constant size of 1.430 mm. and an intermediate stage of digestion corresponding to hunger-stage III of Jackson (1933) is also shown in fig. 1. The lethal lower limit of fat content is about 0.5 mg., and so flies are appreciably

* The relation between the length of the 4th longitudinal vein (X in mm./100) and the dry weight of the blood taken (Y in mg.) is given by

$\hat{Y} = 0.46x - 58.8$ (unpublished data)

nearer to starvation in the dry season than in the wet season. It would be of interest to know the annual changes of nutritional state in females, but such determinations were not possible because of the difficulties of collecting samples of females, only now beginning to be solved, and because the fat content of females is so complicated by pregnancy as to render any simple technique such as was used in this investigation out of the question. We are thus obliged for the

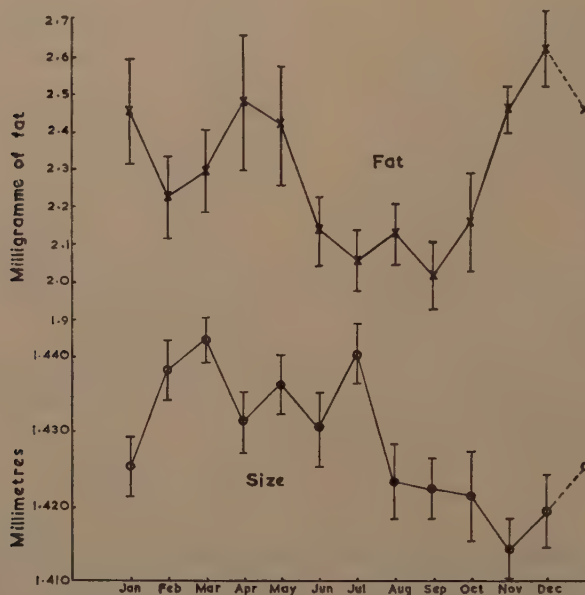


Fig. 1.—Annual variations in size (vein length) (in mm.) and fat (mg.) in *G. swynnertoni*. The incomplete years 1945, 1951 and 1952 have been omitted from the computation of size. All data have been included in the fat curve. The fat values are corrected to a size of 1.430 mm. and to 12.9% RBM (see text). The precision of the observations is indicated by the vertical lines showing one standard error above and below each value.

present to take the fat content of males as an index of female nutrition. It is probable that the latter will be reflected in the size of the offspring, and if we compare the two curves of fig. 1 we see that the marked fall in fat between May and June is followed by a marked fall in mean size from July to August, that the increase in fat content from October to December is followed by an increase of size in the early months of the year, and that the secondary depression in mean size during April and June reflects an earlier depression of fat content.

The detailed comparison between the two curves is complicated by seasonal variations in the time lag appropriate to the comparison. In the cold season the pupal period would be a great deal longer than the approximate figure of 30 days adopted as a mean, and the length of life, which comprises another component of the lag, is known to vary greatly from season to season, although no quantitative estimates of such variations can at present be made. With these qualifications it may be said that the correspondence between the two curves is

a very close one, and since there is abundant evidence from the laboratory that nutritional stress, as reflected in sub-normal fat contents, is associated with the production of small puparia,* there is no reason to doubt that the two reflect different aspects of a single phenomenon, namely the occurrence of seasonal variations in the intensity of nutritional stress.

The climate of Shinyanga.

Seasonal variations in climate are illustrated in fig. 2; on the basis of rainfall and sunshine the year can be divided into two main seasons—the dry season with

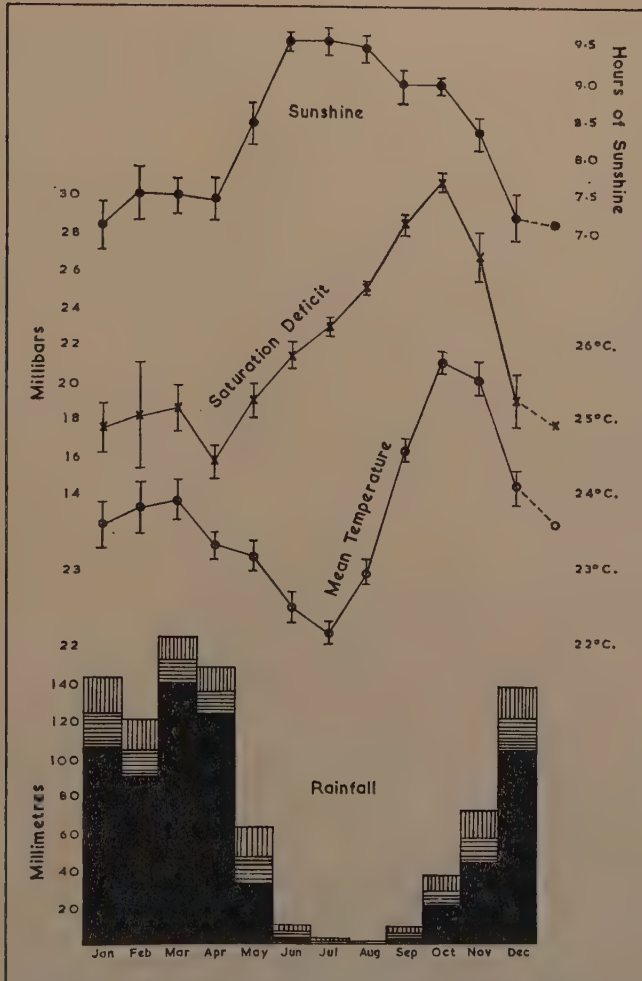


Fig. 2.—The climate of Shinyanga; means of 13 years, 1946–58. The mean values are plotted \pm one standard error (shown by a vertical line or, in the case of rainfall, shaded areas).

* See, for example, Jackson (1937) for failure to synthesize fat, and Willett (1953) for production of small offspring.

less than 25 mm. of rain per month and with 9 or more hours of sunshine per day (June to October inclusive), and the wet season with over 50 mm. of rain per month and with 8 hours or less sunshine per day. The occurrence of a 'short' dry season at the beginning of the year is not well illustrated because its onset varied greatly from year to year; but its existence is indicated by the tendency for February rainfall to be low. May and November are the months of transition between wet and dry seasons, notably in respect of sunshine and rainfall. However, May is in *facies* part of the rains, with long grass, all trees in leaf and surface water abundant, and November in the same way belongs to the dry season, so that it is convenient to divide the year into two equal portions, wet, December–May, and dry, June–November.

Comparison of fig. 1 with fig. 2 shows a striking correspondence between fat content and the season. Fat content was low during the early dry season, high during the rains and intermediate in the short dry season.

Seasonal changes in mean temperature and in saturation deficit are also shown in fig. 2; both rise progressively in the course of the dry season and fall at the break of the rains to an intermediate level, which is maintained till the middle of the long rains; there is a drop in April, after which the saturation deficit rises while temperature falls to its minimum in July. It is clear that neither of these factors can be related to the nutritional stresses discussed above, for at the time when both show maximal rates of increase (between July and October) fat content is approximately constant. In view of this, the association between the decrease in temperature and saturation deficit and the increase in fat content from October to December must clearly be ascribed to coincidence.

Long-term changes in the mean size of G. swynnertoni.

Since about 1951 there has been a marked decrease in the size of examples of *G. swynnertoni*, as shown in fig. 3. Dividing the year into two parts on the

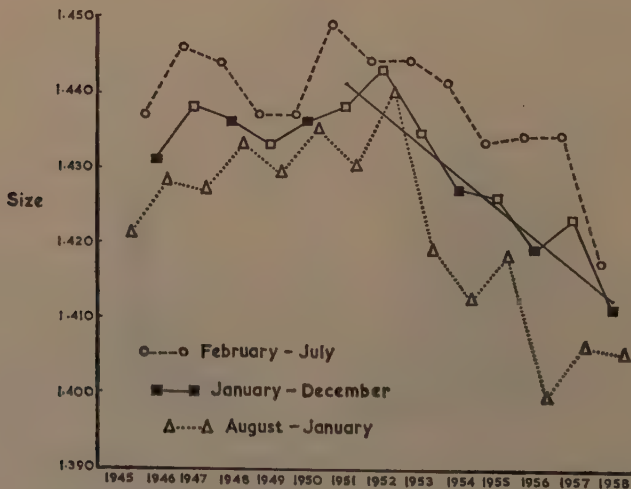


Fig. 3.—The long-term changes in size (vein length) of examples of *G. swynnertoni*. The points indicated by solid black squares are the means of complete years (12 months). The straight line from 1951 to 1958 represents the regression of size on time (value of regression coefficient, -0.008917 ± 0.0006).

basis of climate (see above) and making allowance for the time lag mentioned on p. 708, we see that most of the decrease in mean size (vein length) over a calendar year is to be attributed to the dry season, the wet-season size showing no marked trend until 1958. The implications of this long-term trend are at present obscure; no comparable trends in climate can be demonstrated, nor do the changes appear to be matched by fluctuations in population density, which has been under continuous observation throughout the period.

Discussion.

The present investigation has confirmed the earlier findings of Jackson (1937, 1953) that populations of tsetse fly are characterised by marked and regular fluctuations in mean size and fat content, such fluctuations being symptomatic of corresponding variations in nutritional stress.

In his interim publication, covering the period October 1945 to December 1948, Jackson (1953) found a marked correlation ($r = -0.68$) between size and the 2-p.m. saturation deficit two months before. For the post-1948 data the correlation coefficient is only -0.41 , with 101 pairs of observations and for all the data together -0.46 with 141 pairs of observations. The difference between the pre-1948 and post-1948 values is just significant ($P = 0.05$) by the z -test, although in view of the complications introduced by serial correlation (Moran, 1952) we are doubtful of its validity. Nevertheless, it is clear that the consideration of much additional data has weakened rather than strengthened the correlation, and this, together with the obvious lack of detailed correspondence between nutritional state and saturation deficit already pointed out, makes us suspect that the relation between the two is fortuitous, reflecting no more than that saturation deficit tends to be high in the dry season when nutritional stress is severe, and *vice versa*.

Indeed, in attempting to define the conditions responsible for these variations in nutritional stress, it is surely idle to single out one particular aspect of one particular complex of the environment, however closely it may happen to be correlated with the feature under investigation. The dry season contrasts with the rainy season in many ways not readily susceptible to direct measurement; usually grass fires run through the country in June or July, and in the same months many deciduous trees shed their leaves and many temporary supplies of water become exhausted. Such events are more likely to be important to *G. swynnertoni* than the concomitant fall in temperature or rise in saturation deficit, since they influence the activities of the mammalian hosts of tsetse (Harrison, 1936) and the number of enemies that prey on it (Southon, 1959), at the same time that the amount of shade in the general woodland is restricted. The life-history of the tsetse, in fact, is so closely interwoven with other ecosystems, plant, invertebrate and vertebrate, each affected in multifarious ways by climate, that the possibility of any simple chain of cause and effect existing between any property of the tsetse population and any aspect of the climate is a singularly remote one. The behaviour of the fly itself differs from season to season (Lloyd, 1935) and so does the distribution of its pupae (Burt, 1952); when it is further considered that the samples on which studies of the tsetse fly are based have been shown to be subject to bias in respect both of fat content (Bursell, *in press*) and of size (Jackson, 1948), the problem of accounting for the observed fluctuations is seen to be a truly formidable one. No service is rendered by rationalising specious correlations with particular aspects of the environmental complex into the form of an 'explanation' by implying, for instance, that flies have low fat contents (or are small, or few) 'because' the saturation deficit is high. Such 'explanations', explicit or implicit, abound in tsetse literature, the correlation coefficient being one of the most widely used statistical tools in the field (*e.g.*, Buxton, 1955, Chap. 8). The demonstration of a 'significant' correlation should

be the beginning, not the end, of such investigations, since it is essential to establish whether the causal chain postulated as linking the variables does in fact exist. In so far as it has tended to inhibit research, rather than to stimulate it, the technique of correlation has thus been of questionable value. Alternative methods for the investigation of tsetse ecology may not lie ready to hand, but it is certain that little progress can be hoped for in elucidation of the problem as a whole unless effort is directed towards the elaboration of such techniques.

Two lines of investigation suggest themselves at this stage. On the one hand, tsetse could be reared in the laboratory under controlled conditions and the effect of changing one variable, such as temperature, humidity or light, ascertained. Such studies have not been popular because laboratory-reared tsetse are recognised as so abnormal that conclusions can be drawn from them only with great caution. Nevertheless they might be worth trying since they are the logical successors to the field observations that show correlations between tsetse and climatic factors. On the other hand, one might try to find out what the dry season really means to *G. swynnertoni* in terms of perching places, frequency of host encounter and numbers of predators. Such studies were in fact started respectively by Isherwood (1957), Harley (1958) and Southon (1959).

Summary.

(1945-1958)

A population of *Glossina swynnertoni* Aust., at Shinyanga, Tanganyika, has been studied in respect of size and fat content of non-teneral males by monthly samples over a period of 13 years.

Flies are large from February to July and small from August to January, and this change in size suggests an effect of the wet season (December to May) and dry season (June to November) upon the parent females, allowing for the time-lag of two months representing pupal development and mean age of adult males at capture. Male flies have more fat in the rains and less in the dry season and it is possible that similar changes in the nutritional status of females are responsible for the observed size changes.

The correlation found in earlier work between the size of male flies in any month and saturation deficit two months earlier is confirmed, but reasons are given for rejecting a simple causal interpretation of this correlation.

Since 1951, there has been a progressive decrease in size of *G. swynnertoni* in the area studied, more especially as regards those produced in the dry season.

References.

- BURRELL, E. (1960). The measurement of size in tsetse flies (*Glossina*).—*Bull. ent. Res.* **51** pp. 33-37.
- BURRELL, E. (in press). The behaviour of tsetse flies (*Glossina swynnertoni* Austen) in relation to problems of sampling.—*Proc. R. ent. Soc. Lond.* (A) **36**.
- BURTT, E. (1952). The occurrence in nature of tsetse pupae (*Glossina swynnertoni* Austen).—*Acta trop.* **9** pp. 304-344.
- BUXTON, P. A. (1955). The natural history of tsetse flies.—*Mem. Lond. Sch. Hyg. trop. Med.* no. 10, 816 pp. London, Lewis.
- HARLEY, J. M. B. (1958). Host relationships of *Glossina swynnertoni*.—*Rep. E. Afr. Tryp. Res. Org.* 1956-57 pp. 67-70.
- HARRISON, H. (1936). The Shinyanga game experiment: a few of the early observations.—*J. Anim. Ecol.* **5** pp. 271-293.

- 82 ISHERWOOD, F. (1957). The resting sites of *Glossina swynnertoni* Aust. in the wet season.—*Bull. ent. Res.* **48** pp. 601–606.
- JACKSON, C. H. N. (1933). The causes and implications of hunger in tsetse-flies.—*Bull. ent. Res.* **24** pp. 443–482.
- 42 JACKSON, C. H. N. (1937). Some new methods in the study of *Glossina morsitans*.—*Proc. zool. Soc. Lond.* **1936** pp. 811–896.
- 89 JACKSON, C. H. N. (1946). An artificially isolated generation of tsetse flies (Diptera).—*Bull. ent. Res.* **37** pp. 291–299.
- JACKSON, C. H. N. (1948). Some further isolated generations of tsetse flies.—*Bull. ent. Res.* **39** pp. 441–451.
- 39 JACKSON, C. H. N. (1953). Seasonal variations in the mean size of tsetse flies.—*Bull. ent. Res.* **43** pp. 703–706.
- 25 LLOYD, H. M. (1935). Notes on the bionomics of *Glossina swynnertoni*, Austen.—*Bull. ent. Res.* **26** pp. 439–468.
- MORAN, P. A. P. (1952). The statistical analysis of game-bird records.—*J. Anim. Ecol.* **21** pp. 154–158.
- SOUTHON, H. A. W. (1959). Studies in predation on *Glossina*.—*Rep. E. Afr. Tryp. Res. Org.* 1958 pp. 56–58.
- WILLETT, K. C. (1953). The laboratory maintenance of *Glossina*. I.—*Parasitology* **43** pp. 110–130.

A TECHNIQUE FOR THE TOPICAL APPLICATION OF POISONS TO NON-ANAESTHETISED HOUSE-FLIES FOR KNOCKDOWN ASSESSMENTS.

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LB.

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When a spraying technique is used to assess 'knockdown', the amount of insecticide picked up by the flying insects varies and is very difficult to determine. For this reason, topical application, whereby each insect is treated with a given dose of poison, would be preferable, but till now was unsuitable for measuring knockdown, because there was no efficient method to immobilise the insects during dosing. Anaesthetics (Fisher, 1952; Perry & Hoskins, 1951; Williams, 1946; Wilson, 1949), or cooling (Heal & Menusan, 1948; K. A. Lord, private communication) affect the response of the insects to the insecticides, and using suction to immobilise the insects during dosing (Hewlett, 1954; Kerr, 1954; G. D. Glynne-Jones, private communication) means that the insects have to be handled individually, which is laborious and time-consuming.

The method now to be described is rapid; the treatment time of a batch of ten insects seldom exceeds ten seconds, and the total handling time is about three minutes. The difference between the dosing time of the first and last insects of a batch is negligible and the knockdown can be assessed within 15 minutes of dosing.

General procedure.

House-flies, *Musca domestica* L., of a known age are sucked through a specially designed aperture from a contractible cage on to a suction pad fitted on the hose of a vacuum cleaner. The insects, immobilised by suction, are sexed, the males discarded and the females dosed by a measured-drop apparatus. The females are later removed from the suction pad to glass tubes, when they can be inspected either immediately or after any desired interval.

Apparatus.

The apparatus consists of a suction platform connected to a vacuum cleaner, a specially designed fly cage and a measured-drop apparatus.

(i) The suction platform (fig. 1).

The suction platform consists essentially of a circle of terylene gauze, $2\frac{1}{4}$ inches in diameter, on which the flies are held by suction during treatment. It is made of five parts: the base, the inner cylinder, the suction pad, the suction-pad holding ring, and the movable ring.

The base consists of a flat circular aluminium disc which is connected to the hose of a vacuum cleaner. It is $2\frac{1}{4}$ in. across, and has a central hole 1 in. in diameter. Stuck to the base and at right angles to it is the inner cylinder, a perspex cylinder $1\frac{3}{4}$ in. high, covered at the free end by a tightly stretched terylene gauze, the suction pad, which is held in position by an outer ring, the suction-pad holding ring, $\frac{1}{2}$ in. high. A second outer ring, the movable ring, $1\frac{1}{4}$ in. high, which lies between the base and the suction-pad holding ring, can be rotated round the inner cylinder. A slit, 1 in. long and $\frac{1}{4}$ in. across, bored through the inner cylinder

and the movable ring forms the adjustable air leak (air flow regulator). The wall thickness of the inner cylinder and the suction-pad holding ring is $\frac{1}{8}$ in., that of the movable ring $\frac{1}{4}$ in.

(ii) *The vacuum cleaner.*

An Electrolux vacuum cleaner, Model 62, with an air flow of 60 cu. ft. of free air per minute and a suction pressure of 60 in. on a water gauge, was used.

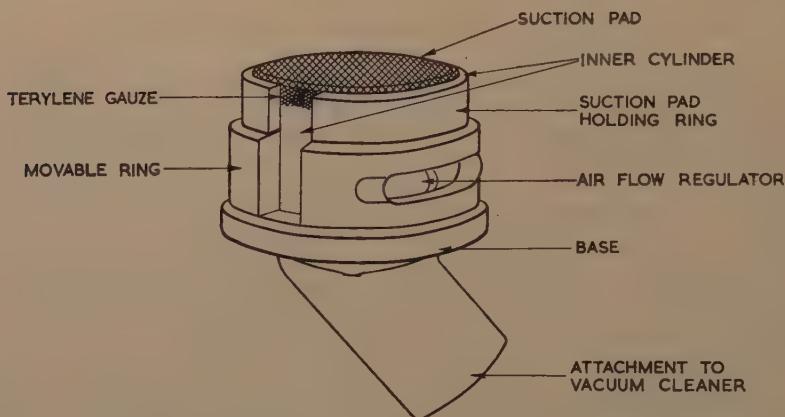


Fig. 1.—Suction platform (a part of the outer cylinders has been removed to show the inner cylinder).

(iii) *Supporting arm.*

A supporting arm, modified from an 'Anglepoise' table lamp with the bulb and shade removed, is clamped to the hose close to the suction platform and carries the weight of the heavy hose, which would otherwise restrict the accuracy of movement of the operator during dosing.

(iv) *The fly cage (fig. 2).*

The fly cage contracts, so that the flies can be crowded together in a confined space, from which they are removed by suction. Crowding increases the chances that insects will be selected at random.

The fly cage consists of five panels and a base. The assembled panels are held together by nuts and bolts. Each panel is made of a wooden frame 1 in. square in cross-section covered by wire gauze. The top panel is 11 in. square, two of the side panels are 11 in. long and 9 in. high. The other two side panels are 9 in. square. When unscrewed, one of the smaller side panels can be pushed inwards, so decreasing the volume of the cage.

(a) *The emergence hole.*—The emergence hole consists of a $2\frac{1}{2}$ -in. hole in the gauze of the side panel (9 in. square), a truncated polyethylene funnel, a pair of perspex funnel holding plates, a perspex cylinder and two aluminium gates.

The truncated funnel abutting against the wire gauze round the circular hole is held in position, at right angles to the gauze, by two perspex plates. The truncated end of the funnel fits into a perspex cylinder 1 in. long and 2 in. in diameter which itself fits tightly into a funnel holding plate. A pair of thin aluminium gates, 2 in. in diameter, slide into guide slits set $\frac{1}{2}$ in. apart on the

cylinder. The gate nearest the truncated end of the funnel has a central hole $1\frac{1}{2}$ in. across, which is covered by a closely woven nylon gauze.

(b) *The sleeve entrance.*—The sleeve entrance is set on the other of the smaller side panels, opposite the emergence hole. It is rectangular, $3\frac{1}{2}$ in. by 6 in. Its base is set about 3 in. from the bottom of the panel, and about half an inch lower than the emergence hole. The nylon sleeve is about 1 ft. long, and during the experiments is tied at its free end.

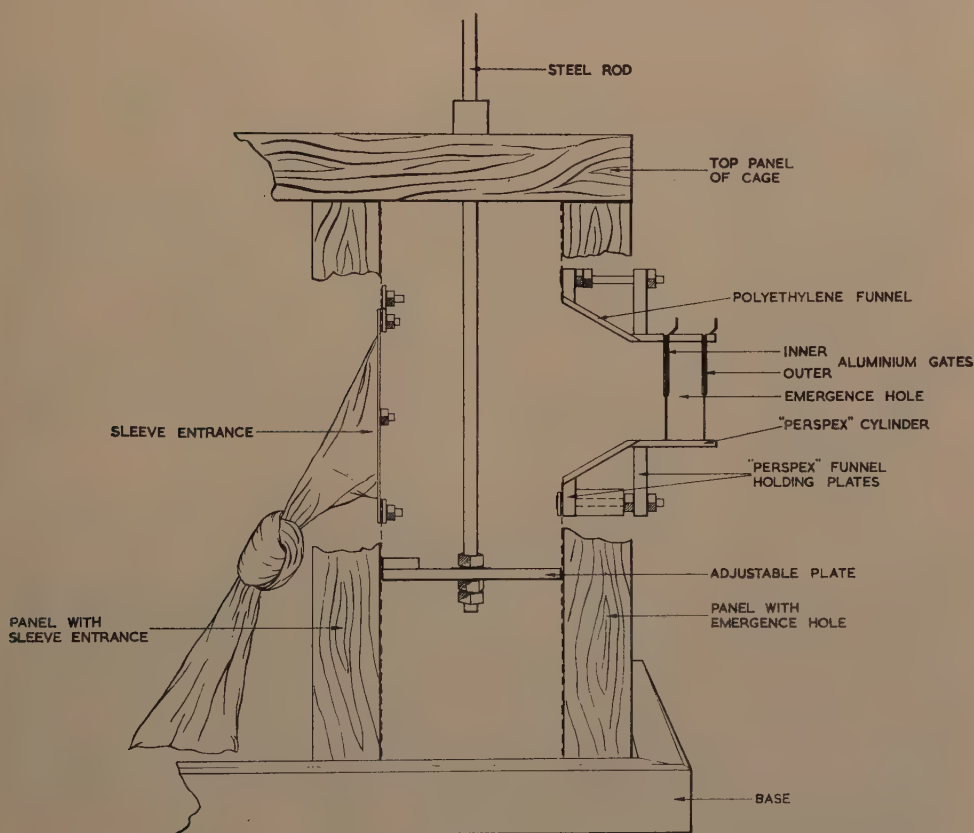


Fig. 2.—Diagram of the contractable fly cage. (The side panel has been removed. The panel with the sleeve entrance has been pushed against the adjustable plate, which has been lifted.)

(c) *Adjustable plate* (fig. 2).—The adjustable plate is made of aluminium, 9 in. long, 2 in. wide and $\frac{1}{4}$ in. thick, to which are screwed, near either end, steel rods 1 ft. long which protrude through the gauze of the top panel. When not in use, the plate lies on the base of the cage, next to the panel with the emergence hole. In order to increase the density of the flies during the experiment, the volume of the cage is decreased by pushing the side panel inwards up to the adjustable plate. When the volume needs to be further decreased, the plate can be lifted to the level of the sleeve entrance. This need not be done when the cage contains many flies.

Testing procedure.

The vacuum cleaner is switched on, the hose clamped to the supporting arm and a square of gauze is fixed to the suction pad by an elastic band, which fits round the suction pad holding ring. The inner aluminium gate is then lifted, allowing the insects to fly from the cage into the cylinder. When enough insects are in the cylinder, the inner gate is closed, the outer one opened, the suction pad placed at the free end of the cylinder, and the insects sucked on to it. When only a few insects enter the cylinder, either the sleeve may be shaken inside the cage and then gently pushed into the cylinder, or both gates may be withdrawn, the suction pad applied to the cylinder and the insects sucked directly from the cage.

Once on the suction pad, the insects are sorted, and the males picked off with a pair of forceps and rejected; the females are turned on their backs with a camel-hair brush, the wings becoming spread and flattened on either side of the body. In this position the limbs are pressed against the gauze, leaving the whole of the thoracic sternites uncovered. The air flow regulator is adjusted while the suction pad is being brought under the syringe. It is opened enough to allow the insects to lift their heads and thoraces slightly off the pad, but enough suction must be retained to prevent them from flying off. The insects are then dosed with a 0.125- μ l. drop of liquid using an Agla syringe. After all the flies have been dosed, a glass specimen tube ($4 \times 1\frac{1}{2}$ in.) is placed over the suction pad, the elastic band holding the gauze is removed, the gauze itself is lifted off the pad with the glass tube and secured with an elastic band. In this way the flies are trapped inside the tube. The time of dosing is recorded for each tube, knockdown is assessed 15 minutes after dosing, or earlier if required, and the number dead is counted on the next day.

Size of batch.

It is not advisable to dose more than 8 to 12 insects in each batch. Not only is it difficult to deal with more flies on the pad because some may escape, but it is also difficult to turn the flies on to their dorsal surface when they are crowded; another reason, already referred to in the introduction, is that differences in time of applying the insecticide becomes appreciable when a batch contains many flies. In practice, with batches of about ten insects, the average dosing time was between 5-7 seconds, which is equal to 0.6-0.8 per cent. of the time between dosing and assessing knockdown. It seldom exceeded 10 seconds, which is only a little more than one per cent. of the total time between applying the insecticide and assessing its effect 15 minutes later. The differences in time of applying insecticide can therefore be ignored when batches of ten flies are treated.

Examination of factors affecting the technique.

Effect of suction on the insects.

The flies look somewhat maltreated when they are on the suction pad; their wings are crumpled, they are tightly pressed to the gauze, and their abdomina are flattened, but the ovipositor was never seen extruded, which is a sign of heavy pressure on the abdomen. When suction is stopped, the flies fly off immediately, and neither the wings nor the limbs show any sign of injury or damage. They remain alive and fully active without food for 24 hr. at 20°C., after having been subjected to suction for more than two minutes. The females lay eggs, which are viable. It can therefore be said that the flies are not seriously affected by suction.

Effect of suction on the spread of the measured drop.

It is likely that the greatest chance of error is the possibility that part of the insecticide dose applied to the insect may be removed by the flow of air

when the flies are treated on the suction pad. This problem was studied by dosing the flies under ultra-violet light, using solutions of fluorescent dyes.

Three different solvents were used: acetone, cellosolve (ethylene glycol monomethyl ether), and odourless distillate. The following fluorescent dyes were used: Oil Colour 5G, Oil Colour 7G (Fine Dyestuffs and Chemicals), and Tinopal PCRP (Geigy).

Each of the dyes was only slightly soluble in odourless distillate, and the spread of the dye on the body of the flies could not be detected accurately when they were used singly. A freshly prepared solution of the three dyes mixed together gave good results and showed up very well under ultra-violet light. Female house-flies, five to six days old, were used for the tests. The flies were sucked on to the pad in the manner described above and each was dosed with a 0.125- μ l. drop of the fluorescent solution. Preliminary experiments showed that, with larger drops, some of the solution leaked on to the suction pad. A piece of muslin was substituted for terylene, which was less absorbent than muslin and slightly fluorescent. The flies were kept on the gauze for about a minute after dosing (during normal experiments fewer than 20 seconds are needed to remove the flies from the pad) and were removed from it with a pair of forceps. The gauze was then scrutinised for traces of fluorescence. The dye mixture produced a very bright yellow fluorescence, which was in sharp contrast with the blue light emitted from faeces and body fluids of the insects. To avoid losing solution by evaporation, the measured drop was applied only when the needle was in contact with the thorax of the insect.

When the air flow regulator was fully closed, fluid sometimes spread to the pad when the drop was applied either to the side of the thorax, or on the prothoracic instead of the mesothoracic sternite. There was no such spread on the pad when the air flow regulator was opened enough to allow the flies to lift their heads and thoraces slightly from the gauze, while remaining attached to it by their wings and abdomen.

The effect of suction on the spread of different solvents on the body of the insects was also examined by means of this technique. When acetone containing the three fluorescent dyes was applied to the mesothoracic sternite of the fly, the solvent evaporated immediately. When the solvent was cellosolve, which has a boiling point intermediate between that of acetone and odourless distillate, the dye also remained localised at the site of application, although it sometimes spread over a limited part of the ventral side of the thorax. With odourless distillate, the whole of the thorax, except for the dorsal plate, was covered by a thin film of the dye, none of which spread on to the gauze. The spread of the solvents was also investigated with flies anaesthetised with ether, placed on a filter paper, and not subjected to suction. Surprisingly enough, no detectable differences were obtained. When odourless distillate was used, the dye spread very rapidly over the thorax, but again did not spread on to the filter paper.

Knockdown and mortality assessment.

The flies can be checked for knockdown either once, *e.g.*, 15 minutes after dosing, or several times, at fixed intervals, *e.g.*, 5, 10, 15 and 30 minutes after dosing. They are subsequently checked 24 hr. after dosing to assess mortality, or later if the poison acts slowly. The end-point can be defined as the time after which no further insects die or recover from the action of poison (Beard, 1949).

For assessing knockdown, the flies are classified either as affected or non-affected, and, to assess mortality, the method of Tattersfield & Potter (1943) is used. All the flies that are partially paralysed but still capable of flight are classified as non-affected. Included in this group are flies with two or sometimes even three limbs paralysed, or those which are only momentarily paralysed.

In general, the flies that are not affected tend to congregate on the gauze, the partially paralysed try to crawl towards the top of the tube, and the affected remain at the bottom. Assessment is made easier by doing it in a partially darkened room and placing a light above the tubes containing the treated insects.

Dosing and assessing knockdown should always be done at a constant temperature and illumination. The flies should all be of the same age to within 12 hr. or less.

Randomisation.

Unless the flies are anaesthetised they cannot be completely randomised. Kerr (1948) found that the males are more active than females, and that their activity was increased by starving for a period of three hours. As the males are more active, many more of them than of females tend to be sucked on to the pad at the beginning of the experiment, and the ratio of males to females changes towards the end, when the cage contains only a few flies. It is also probable that since relative activity governs the ratio of the sexes taken on the pad, the relative activity of the individual females will govern the stage at which they reach the pad; and final batches will be liable to be of less active individuals.

To get the maximum amount of random selection it is advisable to starve the insects for three hours before the experiment, and to shake the sleeve from time to time during the experiment.

Experimental results.

Repeated experiments with this technique under identical conditions give consistent results which should show only small variations. An example taken from two such experiments will illustrate the small variability.

The knockdown activity of a 25 per cent. pyrethrum extract was determined on 27th May 1959 and 1st June 1959 on female house-flies between 5 and 6 days old from different populations but coming from the same stock. Each insect was dosed with a 0.125- μ l. drop of a solution of pyrethrum extract in odourless distillate (boiling range 200–250°C.) from aromatics. At this dose the solvent was non-toxic to controls (50 flies). The extract was tested over a range of four concentrations; four to five replicates, i.e., between 35 and 45 insects, were used for each concentration. The tests were done at 20°C. and knockdown was assessed 15 minutes after dosing. In both experiments the insects were exposed to a light of the same intensity, they had been kept at 20°C. for 24 hr., and starved for three hours before the experiment began. The results, analysed statistically using the probit method of analysis (Finney, 1947), are shown in Table I.

TABLE I.

Determination of the knockdown activity of a commercial 25 per cent. pyrethrum extract, 15 minutes after dosing. Comparison of data from two experiments.

Date of experiment	KD50*	log (KD50 \times 10) and S.E.	Slope of line and S.E.	$\chi^2_{1\%}$
(i) 27.v.1959	0.31	0.50 \pm 0.045	2.95 \pm 0.26	0.38
(ii) 1.vi.1959	0.36	0.55 \pm 0.039	3.78 \pm 0.76	0.33

Formulae for regression lines— (i) $Y = 5.50 + 2.95(x - 0.67)$

(ii) $Y = 5.54 + 3.78(x - 0.69)$

where Y = probit of percentage knockdown

x = log (concentration \times 10)

There is no significant departure from parallelism between the two lines.

Treatment differences are not significant.

In each test about 180 insects were used.

* KD50—% concentration (w/v) of pyrethrins knocking down 50 per cent. after 15 minutes.

Discussion.

The apparatus and technique described makes it possible to handle, immobilise and treat with a known amount of poison, batches of highly active insects, without any cooling or anaesthetics, and without apparently damaging them or affecting their metabolism. The technique is therefore suitable for assessing both the toxicity and the knockdown capacity of an insecticide.

Unless the dose is placed very accurately, or when the insecticide is very volatile, some of the substance applied to the insects may be lost because of the suction used to immobilise them. When knockdown is being assessed, care must also be taken to limit the number of insects in each group, to make unimportant the difference in length of time between dosing and assessing of knockdown for the members of the group.

The degree of randomisation in selection of flies from the cage is not considered to be very satisfactory, and no way has yet been found to ensure completely random selection.

Although by no means perfect, the technique offers a solution to the problem of immobilising active insects when applying insecticides topically. It has primarily been designed for use with house-flies but would be suitable with minor modifications for other species of active insects.

Summary.

An apparatus and technique are described for handling, immobilising by suction, and individually dosing house-flies, *Musca domestica* L. The apparatus consists of a suction platform connected to a vacuum cleaner, a specially designed cage and a measured-drop apparatus. The suction platform consists essentially of a circle of terylene gauze, on to which the flies are drawn from the cage and held by suction during treatment. The cage can be made to contract, so that the flies may be crowded together near the special emergence hole through which they are to be withdrawn. The technique avoids the use of cooling and anaesthetics, which affect the metabolism of the flies, and is therefore especially suitable for measuring knockdown, although it can equally be used to estimate toxicity. Some factors likely to influence the results are examined and discussed, and an example is given of two experiments with house-flies, to show that the method gives reproducible results.

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References.

- BEARD, R. L. (1949). Time of evaluation and the dosage-response curve.—*J. econ. Ent.* **42** pp. 579–585.
- FINNEY, D. J. (1947). Probit analysis. A statistical treatment of the sigmoid response curve.—256 pp. Cambridge, Univ. Press.
- FISHER, R. W. (1952). The importance of the locus of application on the effectiveness of DDT for the house fly, *Musca domestica* L. (Diptera: Muscidae).—*Canad. J. Zool.* **30** pp. 254–266.
- HEAL, R. E. & MENUSAN jr., H. (1948). A technique for the bloodstream injection of insects and its application in tests of certain insecticides.—*J. econ. Ent.* **41** pp. 535–543.

- HEWLETT, P. S. (1954). A micro-drop applicator and its use for the treatment of certain small insects with liquid insecticide.—*Ann. appl. Biol.* **41** pp. 45-64.
- KERR, R. W. (1948). The effect of starvation on the susceptibility of houseflies to pyrethrum sprays.—*Aust. J. sci. Res. (B)* **1** pp. 76-92.
- KERR, R. W. (1954). A method for the topical application of small measured doses of insecticide solutions to individual insects.—*Bull. ent. Res.* **45** pp. 317-321.
- PERRY, A. S. & HOSKINS, W. M. (1951). Synergistic action with DDT toward resistant house flies.—*J. econ. Ent.* **44** pp. 839-850.
- TATTERSFIELD, F. & POTTER, C. (1943). Biological methods of determining the insecticidal values of pyrethrum preparations (particularly extracts in heavy oil).—*Ann. appl. Biol.* **30** pp. 259-279.
- WILLIAMS, C. M. (1946). Continuous anesthesia for insects.—*Science* **103** p. 57.
- WILSON, C. S. (1949). Piperonyl butoxide, piperonyl cyclonene, and pyrethrum applied to selected parts of individual flies.—*J. econ. Ent.* **42** pp. 423-428.

REARING *PSEUDOTHERAPTUS WAYI* BROWN (COREIDAE) A PEST OF COCONUTS IN EAST AFRICA, AND EVALUATION OF ITS SUSCEPTIBILITY TO VARIOUS INSECTICIDES.

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The Coreid bug, *Pseudotheraptus wayi* Brown, formerly known as *Theraptus* sp., is a serious pest of coconuts in the East African territories of Kenya, Tanganyika and Zanzibar. Both adults and nymphs feed on female flowers and on nuts causing deep necrotic lesions and premature nutfall (Way, 1953; Vanderplank, 1953). Work on insecticidal control measures has been complicated by the difficulties involved in spraying the crowns of coconut palms, the majority of which are over 40 ft. from the ground, and by difficulties encountered in assessing *Pseudotheraptus* populations and yield losses (Vanderplank, 1958; Yeo & Foster, 1958). In addition, it has been found that plots used in spray trials must each be of 50 acres or more in size, otherwise excessive interference occurs due to movement of adults of *Pseudotheraptus* between plots. Insecticidal field trials are thus both difficult and expensive, and it became clear that in order to reduce their number to a minimum it was of paramount importance to perfect techniques for bioassay studies with *Pseudotheraptus* so that preliminary screening of insecticides could be undertaken in the laboratory.

The present paper describes a method evolved in Kenya for the large-scale rearing of *Pseudotheraptus*, outlines the technique used for comparing the toxicities of various insecticides to *Pseudotheraptus*, and records the results obtained. It is intended to describe techniques used and results obtained with *Pseudotheraptus* in the bioassay of residual deposits of insecticides on coconut in a later paper.

Method of rearing.

Way (1953) reared *Pseudotheraptus* in small numbers by caging them with fresh coconut spadices, one to four months old, placed in jars of water in a covered outdoor insectary, fresh spadices being supplied twice a week. Tait (1954) and Vanderplank (unpublished) have also reared *Pseudotheraptus* in this manner. The author tried this method and found it had many disadvantages. Chief amongst these was the difficulty and expense of obtaining large numbers of fresh spadices in Kenya where there are no government plantations. Mortalities of first- and second-stage nymphs were very high, and this was thought to be largely due to the fact that many newly hatched nymphs failed to reach the spadix from the walls of the cage where the eggs were normally laid.

K. S. McKinlay maintained a small colony of *Pseudotheraptus* at Tanga by feeding them on young abscissed nutlets from which the bracts had been removed, and after seeing this the author developed the following technique for rearing *Pseudotheraptus* on a comparatively large scale in a wire-gauze outdoor insectary at Matuga, near Mombasa.

Adults were kept in wood-framed cages, each 18 in. x 18 in. x 24 in. high. The floor and roof were of wood, whilst the sides and back were covered by thick white drill. The lower portion of the front consisted of a door, hinged to allow a shallow tray containing the food supply to be removed; the upper portion was covered with wire gauze and was provided with a door (6 in. x 6 in.) through which the adults were introduced. Every two days the food tray was removed

and the old nutlets replaced by fresh ones. Eggs were normally laid on the walls of the cage, where they were left to hatch out. On occasions, egg-laying took place on the nutlets, and these eggs were removed, and nymphs hatched out in 3 in. \times 1 in. glass tubes. These and all newly hatched nymphs found on the old nutlets were placed in cages of similar construction, but of dimensions 9 in. \times 12 in. \times 12 in. and, as with the adults, fresh nutlets were supplied every second day.

Originally, drinking water was supplied in petri dishes containing wet cotton-wool covered with filter paper, but this was found to be unnecessary and was discontinued. Mortality of first- and second-stage nymphs still occurred to a limited extent due to the handling entailed in transferring them to fresh nutlets every other day. This was done with a fine camel-hair brush by an African assistant who eventually became reasonably skilful at the work, and mortality of young nymphs was reduced to 10 or 15 per cent. Mortalities of the later nymphal stages were very low, but 1 to 2 per cent. of adults died per day through causes not attributed to old age.

The nutlets used were fallen ones, from 1 to 2½ inches in length, collected daily from coconut plantations, and included some that had abscissed following *Pseudotheraptus* damage as well as others shed from physiological causes. It was advantageous to remove the bracts, particularly in the case of young nymphs, for their stylets were frequently damaged when being forced through the rather tough bracts. Fifty adults could be kept conveniently in each large cage, but raising the number to over 100 led to increased mortality. Approximately 50 nymphs were kept in each small cage.

The duration of the different stages of the life-cycle of *Pseudotheraptus* under these rearing conditions at Matuga, where the temperature and humidity fluctuate very little, is summarised in Table I. These figures are in general agreement with those of Tait (1954).

TABLE I.

Duration of stages in the life-cycle of *Pseudotheraptus wayi*.

	August 1958				April-May 1958			
	Mean temp. 75°F. (Min. 69°, Max. 82°) Length of stages (days)				Mean temp. 79°F. (Min. 73°, Max. 85°) Length of stages (days)			
	No. of individuals	Min.	Max.	Mean	No. of individuals	Min.	Max.	Mean
Egg ..	39	8	9	8.5	50	8	9	8.3
1st instar	31	2	5	3.9	66	2	5	3.5
2nd instar	24	5	8	6.8	50	5	7	5.6
3rd instar	37	4	8	5.4	28	3	5	3.9
4th instar	40	5	8	6.1	24	4	6	4.8
5th instar	54	8	11	9.5	22	7	10	8.4
Mean total duration of egg and nymphal stages				40.2				34.5

Technique employed for the topical application of measured volumes of insecticide to *P. wayi*.

The apparatus used was identical with that described by Glynne Jones & Lowe (1956) and consisted of an Agla micrometer syringe with the micrometer connected to a toothed wheel actuated by a solenoid; there being no electrical

supply at Matuga the solenoid was depressed by hand. A single drop was 0.096 μ l. in volume and the error between single and double drop replicates were calculated by Glynn Jones & Lowe (1956) as 8 and 4.5 per cent., respectively.

The insects treated were in all cases well-fed adults not less than five and not more than 14 days old. It was found unnecessary to anaesthetise the insects when treatments were carried out early in the morning at an ambient temperature of 78–81°F. The insects were held with the pronotum between thumb and forefinger and, immediately prior to the treatment of each insect, one drop was expelled from the syringe on to unglazed paper held at the needle tip to reduce errors caused by evaporation from the needle between doses.

After treatment, the insects were placed in the smaller type of cage with fresh nutlets. Only rarely did an insect attempt to fly after dosing except in the case of pyrethrum, which induced cleaning reflexes and sometimes flight in the few minutes of activation immediately following dosing and before the knockdown occurred. Normally, ten males and ten females were kept after treatment in each 9 in. \times 12 in. \times 12 in. cage and mortality counts were taken at 48 hr., at which time fresh nutlets were provided, and again 72 hr. after dosing. It was found that, for certain of the insecticides, 48 hr. was insufficient time to achieve full mortality results, and thus in all cases the 72-hr. figure only has been used.

The solvent used was odourless distillate of kerosene except in the case of malathion, which was dissolved in 1.5 per cent. acetone:98.5 per cent. odourless distillate of kerosene. The comparatively low volatility of odourless distillate of kerosene ensured a minimum of evaporation from the tip of the hypodermic needle, the bore of which was 0.15 mm., and the surface tension was low enough to enable the drops to spread well on the insect and so minimise the chances of the insecticide being rubbed off before evaporation of the solvent. Toxicity of the solvent to *Pseudotheraptus* at the quantities used was insignificant. A standard dose of six drops (0.576 μ l.) was applied to each insect on the dorsal side of the mesothorax, from where the insecticide filtered under the wings and spread over the dorsal side of both thorax and abdomen. A range of five concentrations and a control using solvent only was used for each insecticide (except for DDT, where eight concentrations were used) and the results subjected to probit analysis (Finney, 1952).

Vanderplank (1959), working with *Pseudotheraptus*, states that addition of a coumarone indene resin to DDT in a 50:50 mixture of power kerosene/diesolene changes the crystallisation characteristics of the formulation to give longer residual toxicity of a more selective character. A supplementary experiment was therefore carried out to determine whether addition of resin improved the toxicity of DDT when applied topically. Five batches of adults of *Pseudotheraptus*, each of ten males and ten females, were treated with single drops (0.096 μ l.) of 0.5 per cent. p,p'DDT (females) or 0.25 per cent. p,p'DDT (males) in 50:50 power kerosene/diesolene applied to the mesonotum. A similar five batches were treated with the same insecticide, to which coumarone indene resin at one-tenth the DDT content had been added.

Results.

These are summarised in Tables II and III. The χ^2 values indicated that the fit of a straight line to the log dosage/probit values was good, except for pyrethrins, for which there were signs of heterogeneity and it was necessary to

introduce an adjustment factor, $\frac{\chi^2}{\text{degrees of freedom}}$, in the calculation of fiducial

limits. Pyrethrins synergised with piperonyl butoxide at eight times the pyrethrins content was included in the tests, and although the formulation was

approximately four times as toxic as unsynergised pyrethrins in the 70–100 per cent. mortality range, results showed a great deal of variation and could not be subjected to statistical analysis; therefore they are not included in Table II.

The regression coefficients of DDT, γ BHC and pyrethrins are close enough to allow valid comparisons of their relative toxicity to *Pseudothraupis* to be based

TABLE II.

Toxicity of various insecticides to *Pseudothraupis wayi*.

Insecticide	Sex	Total no. of adults dosed	Regression coefficient	LD50 in 10^{-6} g.	Fiducial limits of LD50 in 10^{-6} g. (95% confidence)	LD95 in 10^{-6} g.
p,p'DDT	Male	459	2.69	0.397	± 0.001	1.63
	Female	540	2.55	0.850	± 0.012	3.75
Dieldrin	Male	354	4.53	0.0786	± 0.0002	0.181
	Female	354	4.08	0.165	± 0.001	0.418
γ BHC	Male	330	2.98	0.0335	± 0.0001	0.120
	Female	342	2.73	0.0870	± 0.0004	0.349
Malathion	Male	240	6.02	0.317	± 0.001	0.595
	Female	240	5.50	0.555	± 0.001	1.105
Pyrethrins	Female	300	2.67	1.18	± 0.02	4.88

Counts taken 72 hr. after treatment.

TABLE III.

Mortality of *Pseudothraupis wayi* after dosing with DDT, with and without coumarone indene resin, in 50:50 power kerosene/diesolene.

Sex	Dosage	Percentage mortality at 72 hr.						
		Replicates (10 adults per treatment per replicate)					Mean	
		1	2	3	4	5		
♂	0.096 μ l. 0.25% p,p'DDT	80	40	40	50	50	52	
♂	0.096 μ l. 0.25% p,p'DDT plus 0.025% resin	80	50	50	40	50	54	
♀	0.096 μ l. 0.5% p,p'DDT	50	60	50	50	50	52	
♀	0.096 μ l. 0.5% p,p'DDT plus 0.05% resin	60	70	40	40	30	48	

upon their LD50 values. The coefficients for dieldrin and malathion, however, are considerably higher, and the LD95 figures give a more realistic comparison of the insecticides for the practical purposes of selecting insecticides for field trials.

From Table III it will be seen that the addition of resin does not enhance the toxicity of DDT to *Pseudothraupis* when applied topically.

Discussion.

The work on chemical control of *Pseudotheraptus* in Kenya is directed towards finding an effective residual insecticide which can be applied from small hand machines by African climbers. Elsewhere in East Africa, trials with aerosols and residual insecticides applied both from the air and from ground machinery are in progress. There is a requirement, therefore, both for insecticides with a good residual toxicity and for others with a good contact action.

A study of the LD95 values in Table II lead to the following conclusions:—

(1) *Pseudotheraptus* is not very susceptible to pyrethrins, which insecticide can clearly be discarded from future trials.

(2) Toxicity of dieldrin to *Pseudotheraptus* is markedly greater than that of DDT. Past experience on a variety of tropical crops indicates that residual life of these two insecticides is generally of the same order, and it is therefore likely that dieldrin would prove more effective than DDT in residual spraying trials.

(3) Dieldrin is rather less toxic than γ BHC, but, at current market prices, commercial formulations of dieldrin are cheaper than those of BHC. On a price for price basis, therefore, there is little to choose between them. However, experience in the tropics indicates a relatively short residual life for BHC, and this insecticide can be discarded from trials of residual insecticides with some confidence.

(4) Where residual life is of little consequence, *e.g.*, aerosol spraying, there would appear to be little to choose, price for price, between dieldrin, BHC and malathion. DDT, however, is likely to be inferior.

In the past, DDT has been the insecticide most widely used in spraying trials for *Pseudotheraptus* control. Vanderplank (1959) reported that the minimum quantity of a formulation containing approximately 10 per cent. p,p'DDT and 1 per cent. coumarone indene resin, by weight, in a mixture of equal volumes of power kerosene and diesolene required to give 100 per cent. kill of adult females of *Pseudotheraptus* was one 85-micron drop applied dorsally or one 60-micron drop applied laterally. He further states that one 85-micron drop of such a formulation contains 0.31 μ g. of DDT; however this would appear to be a miscalculation as the weight of p,p'DDT in such a drop would be of the order of one-tenth the amount stated. The discrepancy between such an amount, found by Vanderplank to give 100 per cent. kill of adults, and the figure of 3.75 μ g. p,p'DDT found by the author to be required for a 95 per cent. kill is more than one hundred-fold. The cause for such a discrepancy may in part be due to different techniques, and it must be mentioned here that the toxicity of DDT applied in 0.096 μ l. of kerosene/diesolene to the mesonotum was found by the author to be approximately 1.5 times as great as when applied in 0.576 μ l. of odourless distillate of kerosene so as to spread under the wings. The addition of resin to the formulation did not enhance its toxicity when applied topically (see Table III). A difference exceeding one hundred-fold appears, however, a very large one to be accounted for solely in terms of the techniques employed, even though these differed greatly.

Summary.

A method is described for the large-scale rearing of *Pseudotheraptus wayi* Brown, the Coreid causing immature nutfall of coconuts in East Africa.

Adults were kept in cages with sides of thick white drill and wire-gauze, in an outdoor insectary at Matuga, near Mombasa, Kenya, and were provided with freshly collected fallen nutlets from which the bracts had been removed. Eggs were normally laid on the walls of the cage. The nutlets were replaced every two days, and all newly hatched nymphs removed and placed in other cages supplied with fresh nutlets every second day. There was some mortality in the

first- and second-instar nymphs due to the handling entailed when nutlets were replaced, but in the later nymphal stages it was very low. Under these rearing conditions, the life-cycle from egg to adult was completed in from 35 to 40 days.

The toxicities to *Pseudotheraptus* of dieldrin, DDT, γ BHC, malathion and pyrethrins in a solvent were compared by topical application of measured-drop doses from an Agla micrometer syringe in a range of five concentrations (except for DDT, where eight concentrations were used). The mortality counts at 72 hr. were taken as the measure of toxicity.

Analysis of the log dosage/probit regression lines indicated that dieldrin was markedly more toxic than DDT to *Pseudotheraptus*, and that the toxicity to this insect of pyrethrins was of a very low order.

In a supplementary experiment to determine whether the addition of resin improved the toxicity of DDT when applied topically, batches of adults were treated with measured drops of a solution of p,p'-DDT (0.5 per cent. for females, 0.25 per cent. for males) and others with the same concentrations of DDT to which coumarone indene resin at one-tenth of the DDT content had been added. The toxicity of the DDT was not enhanced.

It is concluded that dieldrin would be the most suitable residual insecticide for field trial against *Pseudotheraptus*, and that, for trials as aerosols, dieldrin, γ BHC and malathion are likely, price for price, to give results of the same order, and would be superior to DDT.

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References.

- FINNEY, D. J. (1952). Probit analysis. A statistical treatment of the sigmoid response curve.—2nd edn., 318 pp. Cambridge, Univ. Press.
- GLYNNE JONES, G. D. & LOWE, H. J. (1956). An inexpensive addition to a micrometer syringe for the semi-automatic production of small measured drops.—*Lab. Pract.* 5 p. 69.
- TAIT, E. M. (1954). Some notes on the life-history and habits of *Theraptus* sp. (Coreidae).—*Bull. ent. Res.* 45 pp. 429–432.
- VANDERPLANK, F. L. (1953). Causes of coconut nutfall and gumosis.—*Nature, Lond.* 172 pp. 315–316.
- VANDERPLANK, F. L. (1958). Studies on the coconut pest, *Pseudotheraptus wayi* Brown (Coreidae), in Zanzibar. I. A method of assessing the damage caused by the insect.—*Bull. ent. Res.* 49 pp. 559–584.
- VANDERPLANK, F. L. (1959). Studies on the coconut pest, *Pseudotheraptus wayi* Brown (Coreidae), in Zanzibar. III. A selective residual insecticidal formulation and its effects on the ecology of the insect.—*Bull. ent. Res.* 50 pp. 151–164.

- WAY, M. J. (1953). Studies on *Theraptus* sp. (Coreidae); the cause of the gumming disease of coconuts in East Africa.—*Bull. ent. Res.* **44** pp. 657–667.
- YEO, D. & FOSTER, R. (1958). Preliminary note on a method for the direct estimation of populations of *Pseudotheraptus wayi* Brown on coconut palms.—*Bull. ent. Res.* **49** pp. 585–590.

GROUP EFFECTS ON FEEDING IN ADULT MALES OF THE DESERT
LOCUST, *SCHISTOCERCA GREGARIA* (FORSK.), IN RELATION
TO SEXUAL MATURATION.

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E. H. N.

CONTENTS.

	PAGE
Materials and methods	732
Experiments	733
Young males crowded and isolated	733
Young males in pairs and isolated	741
Young males in pairs with each other and in pairs with mature males	743
Mature males crowded and isolated	746
Late-maturing immature males isolated and kept in pairs with mature males	748
Late- and early-maturing mature males in similar groups	750
Discussion	750
Summary	751
Acknowledgements	752
References	752

It has been shown (Norris, 1954) that sexual maturation in the males of the desert locust, *Schistocerca gregaria* (Forsk.), is accelerated by crowding with individuals of either sex and that the mature male exerts a particularly strong stimulus which is independent of crowding. Single males kept from emergence as adults with one mature male become mature more rapidly than those kept with one young male or with one female, mature or immature. Males kept in isolation with single females often exhibit greatly delayed maturation, the incidence of which is seasonal (Norris, 1957). This delay, which was considered to be a manifestation of a tendency to adult diapause is usually brought rapidly to an end if a mature male is substituted for the female. Isolated males or males paired with single females do not normally assume the bright yellow coloration characteristic of crowded males at maturity. Substitution of a second mature male for the female results in the rapid appearance of the yellow colour. Although crowding with older mature locusts or with locusts of their own age accelerates male maturation it was found that continuous crowding with very young immature locusts (less than one week old) actually retards maturation.

It was thought possible that these group effects on maturation might be related to effects on the activity or on the food consumption of the locusts. It is generally assumed that crowded locusts are more active than isolated ones and that their food consumption is greater, but little experimental work has been done on the subject. Davey (1954) measured the consumption of fresh grass by *Schistocerca* hoppers and adults and there was some indication that hoppers kept in groups of twelve ate more than those kept in groups of three. There were, however, no data as to the effects of crowding on adult consumption. Chauvin (1941) recorded that isolated *Schistocerca* adults ate much less than crowded ones but few figures were given and the ages and state of maturity of the locusts were not stated.

A series of experiments was accordingly carried out in which the quantities of grass eaten and faeces excreted by adults under different grouping conditions were measured. Observations were also made on the behaviour of the locusts with a view to comparing the levels of activity. Some of these behaviour observations involved the same locusts as the feeding observations but as this was not always practicable many separate experiments were carried out, and the results of the activity observations will be published later. The effect on feeding of crowding with very young immature males was not measured as the feeding of a single individual in a crowd of others could not be distinguished.

The work deals entirely with male adults reared as hoppers in crowded conditions. The differences in maturation time under consideration were the result of grouping during adult life and were not perceptibly affected by grouping during hopper life.

The work was carried out during 1955 and 1956 in the laboratory of the Anti-Locust Research Centre which was then in the British Museum (Natural History).

Materials and methods.

The origin of the locusts used in this work, their morphological characteristics and the general laboratory breeding methods have already been described in detail (Norris, 1952, 1957). The breeding room was kept at a constant temperature of approximately 28°C., but 100-watt electric lamps switched on during the day-time raised the temperature in the centres of the cages to about 35°C. The young males were usually removed from the breeding cages within 24 hours of emergence as adults and placed in the required groups in cylindrical celluloid cages. These cages had a total capacity of 12 litres, but a false floor of perforated zinc reduced their capacity to 9 litres. They were grouped in fives round the electric lamps.

The locusts were fed once daily, except on Sundays, with grass grown on a sewage farm near London. Species of *Poa* and *Lolium* predominated in the food, but other species were often present and, as will be seen, great fluctuations in the level of feeding may often have been attributable to these differences.

No attempt was made to estimate the weight of *fresh* grass consumed. All figures given are dry weights. The dry weight consumed was estimated by weighing out as many identical samples of well mixed fresh grass as were required, drying one of them immediately to find the total dry weight and drying the remains of the other samples after they had been fed to the locusts. The dry weight of the sample fed to the locusts subtracted from the dry weight of the control sample represented the approximate amount eaten by the locusts. The grass was dried at a temperature of 60°F. Small errors must arise owing to differences in the proportions of leaf and stalk present in different samples. The method is not sufficiently accurate for estimating the consumption of single locusts but is adequate where, as in the present work, an average for ten or more individually isolated or grouped locusts is required. No attempt was therefore made to estimate the consumption of isolated males separately. They were treated in the same way as the crowded ones, one or more samples of grass being roughly divided between them, and the residue from all their cages being weighed together and the quantity consumed divided by the number of locusts. The quantity of grass provided was always in excess of the quantity eaten and this was particularly so for the isolated ones which had to be given an unnecessarily large quantity so that it did not become too dry before the end of the feeding period. The fresh grass was placed in the cages soon after the lamps were switched on in the mornings.

The dry weight of the faeces expelled was accurately measurable. In any one experiment this bore a fairly consistent relationship to the quantity of grass eaten,

and individual records were in some cases made separately for the isolated individuals, giving results more amenable to statistical treatment. It is appreciated that there are likely to be individual differences in the percentage of food utilised and also in the percentage of different samples utilised. Since, however, the quantities excreted bear, in general, a direct relationship to the quantities eaten, it seems justifiable to regard excretion as a rough indication of consumption, at least when making simultaneous comparisons between members of the same batch of locusts treated in different ways but fed on the same food.

Maturation was recognised by colour change, the criteria used having been fully described in a previous publication (Norris, 1954).

Experiments.

Young males crowded and isolated.

There were four experiments in which the feeding of young males kept in isolation was compared with that of others from the same batch kept in crowded conditions. Observations were begun shortly after emergence and continued for three or four weeks, by which time the crowded males and usually at least some of the isolated ones were mature. Measurements of the dry weight of food eaten and of faeces excreted were made at the end of successive two- or three-day periods (very occasionally four-day) and the mean consumption and excretion per locust per day during the period were calculated.

The locusts set up for observation in the four experiments were as follows:—

Experiment I	10 isolated males/1 crowd of 20 males.
Experiment II	10 isolated males/2 crowds of 5 males/1 crowd of 20 males.
Experiment III	10 isolated males/1 crowd of 10 males.
Experiment IV	10 isolated males/2 crowds of 5 males.

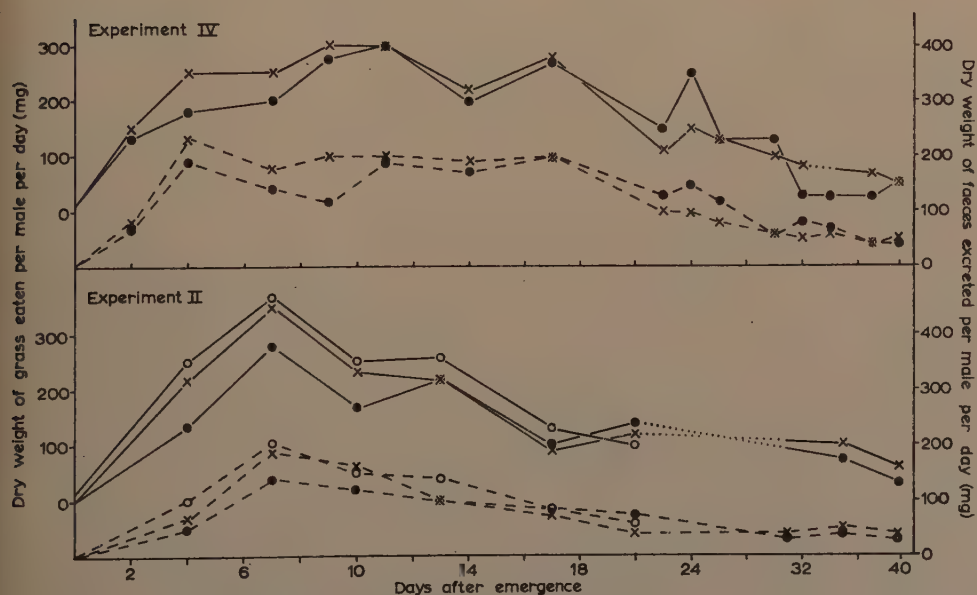


Fig. 1.—Mean daily dry weights of grass eaten and of faeces excreted per adult male when isolated and crowded, respectively. (Experiments II and IV.)

Crowds of 20 males, o; crowds of 5 males, x; isolated males, ●; grass eaten, —; faeces excreted, ----.

TABLE I.

Feeding and excretion of crowded and isolated adult males during the first 3 weeks after emergence
(dry weights of food eaten and of faeces excreted).

Experiment	I				II			
	1st to 10th		11th to 20th		1st to 10th		11th to 20th	
	Crowded (20)*	Isolated	Crowded (20)	Isolated	Crowded (20) (5)	Isolated	Crowded (20) (5)	Isolated
mg. eaten per locust per day	461	346	152	222	287	266	165	146
mg. excreted per locust per day	248	164	84	106	148	136	93	86
Utilisation (%)	46	53	45	52	48	49	44	41

Experiment	III				IV			
	1st to 10th		11th to 20th		1st to 10th		11th to 20th	
	Crowded (10)	Isolated	Crowded (10)	Isolated	Crowded (5)	Isolated	Crowded (5)	Isolated
mg. eaten per locust per day	280	229	227	188	259	214	188	208
mg. excreted per locust per day	176	144	166	123	179	156	151	160
Utilisation (%)	37	37	27	35	31	27	20	23

* Figures in brackets indicate number of males in the crowd. In all experiments, the number of isolated males was ten.

In Experiment I, the locusts were supplied with dry bran as well as grass; in the other experiments grass alone was present. Mean consumption and excretion per locust per day for the first ten days and the second ten days of adult life in the four experiments are shown in Table I. Mean daily consumption and excretion per locust during successive 2- or 3-day periods in Experiments II and IV is shown graphically in fig. 1.

All the locusts showed the normal period of heavy feeding during early adult life which is characteristic of Acridids and which is associated with rapidly increasing body weight. Consumption reached a peak during the second week of adult life and declined thereafter to a fairly steady low level which was reached towards the end of the third or during the fourth week.

In every experiment the crowded males ate more than the isolated ones during the first ten days of adult life. Mean consumption per crowded locust per day during this period varied from 259 mg. in Experiment IV to 461 mg. in Experiment I. Mean consumption per isolated locust varied from 190 mg. in Experiment II to 346 mg. in Experiment I. The level of feeding in Experiment I was much higher than in the other experiments and this was possibly due to the presence of bran. During the first ten days as much bran as grass was eaten, but after the end of the 17th day bran was eaten only in negligible quantities. General laboratory observations confirm the fact that groups of both sexes eat bran voraciously during the first week or two of adult life but that it is little eaten later if the grass supply is adequate. Davey (1954) showed that the hoppers eat bran much less at the beginning and end of the instars than at the middle. It seems, therefore, that it is eaten in appreciable quantities only during periods of rapid growth or weight increase when the appetite is large.

In those experiments where the locusts were fed on grass only, the maximum consumption recorded for any 2- or 3-day period was 441 mg. per locust per day for the 10-male group in Experiment III. The highest figure recorded for isolated males was 337 mg. in Experiment III.

The greatest difference in consumption between isolated and crowded males during the first ten days occurred in Experiments I and II in which the males in groups of 20 ate, respectively, 33 and 51 per cent. more than the isolated ones. In Experiment II, even the males in groups of five ate 40 per cent. more than those in isolation, showing that almost the full effects of crowding were obtained at this low density. In Experiments III and IV, the groups of ten and five males, respectively, ate 22 and 21 per cent. more than the isolated ones during the first ten days. However, the level of feeding declined more rapidly in the crowded than in the isolated males so that at some point the position was reversed. In Experiment I, in which early consumption was particularly high, this point was reached early, at the end of the second week; in Experiments II and IV it was reached at the end of the third week (see fig. 1). In consequence of this reversal, mean consumption during the second ten days of adult life was actually higher for the isolated males in Experiments I and IV and only slightly lower in Experiment II. By the fifth week, when daily consumption had fallen to a low level of between 50 and 100 mg., it again tended to be lower in the isolated males (see fig. 1). The effect of crowding on older mature males is, however, discussed later (pp. 746 to 749). The early decline in feeding of the crowded males is, as will be shown later, associated with their earlier maturity, and in Experiment III, which was exceptional in that the crowd did *not* at first mature more rapidly, they continued to eat at least slightly more than the isolated ones up to the end of the third week, when observations were discontinued. Asket Singh (1957) recorded that *Schistocerca* adults fed on cabbage ate from two to three times as much during the first ten days as during the second ten days and suggested that the decline in feeding was due to approaching maturity.

Since excess consumption by the crowded males during the first ten days after

emergence was a feature of all experiments, the significance of the phenomenon can scarcely be doubted. Statistical confirmation was unfortunately hampered by the great day-to-day variability, both of absolute consumption and of relative consumption between the treatments. This variability was reduced by assessing several days' consumption together, but this procedure had the disadvantage of reducing the number of points for comparison, and in those cases where the period of excess consumption by the crowds was short the difference tended to be not statistically significant although it might, while it lasted, be greater than in other experiments where a smaller difference was maintained for a longer period. This applied to the 20-male group in Experiment I and to the 5-male groups in Experiment II, both of which ate very much more than the isolated males, but only for ten days. Otherwise the differences between the treatments were significant, although in some cases at rather a low level. Tests made to see whether the differences between the pairs of figures for each period differed significantly from zero gave the following results:—

Experiment II	$n = 4, t = 4.605, P < .01.$
Experiment III	$n = 4, t = 3.152, P < .05 > .02.$
Experiment IV	$n = 4, t = 2.955, P < .05 > .02.$

In Experiment II, the two 5-male groups ate very slightly but consistently less than the 20-male groups, and the difference was highly significant ($n = 4, t = 6.818, P < .01$). In Experiment III, where the crowded males continued to eat more than the isolated ones up to the end of the third week, the difference for the whole period was significant ($n = 8, t = 2.331, P < .05 > .02$). In this experiment, the crowded males ate more than the isolated ones at all nine observations but, as was often the case, great variability in the magnitude of the differences lowered the level of significance.

The total weight of dry grass consumed by one crowded male during the first 20 days of adult life in Experiments II, III and IV was, respectively, 4.5, 5.0 and 4.4 g. The figures for the isolated males in the three experiments were, respectively, 4.1, 4.2 and 4.2 g. When, therefore, the whole period is considered, the difference in total consumption between the treatments is small. Davey (1954), working in the same laboratory, estimated that crowded males ate an average of 17.79 g. of fresh grass during the first 20 days of adult life. Since the water content of the fresh grass is usually between 80 and 85 per cent., this would represent a dry weight of from 2.7 to 3.6 g. It is probable that any disparity is due to the fact that in her experiments the grass was kept fresh by standing it in water, whereas in the present case it was allowed to dry between one feed and the next. As will be shown later, there are indications that more grass is eaten when the water content is low.

Estimations of absolute quantities eaten have, however, probably little practical significance since it seems certain that during active life in natural conditions much more food would be required. Weis-Fogh (1952) suggested that flying adults might eat two or three times their own weight of fresh grass daily.

There was no evidence of any significant effect of crowding on the percentage of dry food eaten which was utilised. Excretion, as might be expected, reflected consumption, and in any one experiment the weight of faeces expelled was roughly proportional to the weight of dry food eaten in the corresponding period. Utilisation varied greatly, however, in different experiments. The reason for this variability was not apparent, but in view of the constancy of other environmental factors it was most probably due, like the daily fluctuations in consumption, to differences in the nature of the grass. Utilisation during the first ten days varied in the four experiments from 27 to 53 per cent. (see Table I). In Experiments II and III, the figures for crowded and isolated males were the same; in Experiment I the figure for the isolated males was slightly higher and in Experiment IV

it was slightly lower. There was a tendency for utilisation to drop after the peak feeding period was over, and most of the figures for the second ten days are lower than those for the first ten days. Davey (1954) recorded that, during hopper life, utilisation decreased progressively from the first to the fifth instar. Her figure of 35 per cent. for the fifth-instar hopper is comparable with the lower figures recorded in this work for early adult life.

The percentages of males which were mature by the end of the third week in the four experiments were as follows:—

Experiment I	Crowded	70	Isolated	40
Experiment II	"	(20 ♂♂) 100	"	30
		(5 ♂♂) 80		
Experiment III	"	56	"	56
Experiment IV	"	50	"	10

In Experiment III, some of the isolated males matured very early, but by the middle of the fourth week all the crowded ones were mature and they were, as usual, ahead of the isolated ones in this respect. In Experiments I and II, 40 and 70 per cent., respectively, of the males in crowds of 20 were mature by the end of the second week. It is clear, therefore, that the earlier maturation of the crowded individuals occurs or is at least determined during the period when they are eating more than the isolated ones. Although within one experiment the earlier maturation of the crowded males is associated with higher consumption, there seems to be no correlation between early maturation and high consumption where different batches of individuals are compared. Thus, maturation of the crowded males was earliest in Experiment II, and yet average consumption during the first ten days was almost the same as that of the later-maturing males in Experiment III. In Experiments I and III, the crowded males increased their body weight by 61 and 63 per cent., respectively, during the first two weeks of adult life. In both experiments the isolated males increased weight by 50 per cent. during the same period. In Experiments II and IV, on the other hand, the higher consumption of the crowded locusts was not reflected in their weight increase, which reached 53 and 42 per cent. (58% for the 5-male groups) as compared with 57 and 48 per cent. for the isolated ones. In Experiment II, the excess eaten by the crowd was at the maximum and utilisation was also high. It can only be supposed that for some reason, possibly connected with levels of activity, these locusts required more food.

The above observations suggest that the accelerating effects of crowding on maturation are not directly attributable to its stimulating effect on feeding. This conclusion is borne out by the results of experiments to be described later.

In Experiments III and IV, where maturation of the crowded males was latest, the decline in feeding after the tenth day was less than in the other two experiments. The decline to a low level in the neighbourhood of 100 mg. per locust per day always occurred during the fourth week, at the latest. But early maturation was associated with earlier decline in feeding and this was particularly well illustrated in Experiment IV. By the 25th day, five of the isolated males were mature and five remained immature. For the next three days the weight of faeces expelled by each individual was separately measured. The five mature males each expelled a daily average of from 20 to 40 mg. (mean 34 ± 9) and the five immature ones from 50 to 140 mg. (mean 92 ± 35). The difference was significant ($n = 9$, $t = 3.390$, $P < .01$). One of the 5-male groups in the same experiment became mature before the other. As has been previously recorded (Norris, 1952) maturation in parallel low-density groups from the same batch often tends to show some of the variability which is characteristic of isolated individuals. The males in Group A matured in 17 to 21 days and those in Group B in 23 to

25 days. For the first 17 days the consumption of these two groups was estimated together, but on the 15th day (before any of the males were mature) it was noticed that Group A was obviously eating very much less than Group B. From the 17th day, upon which three males in Group A became mature, the consumption of the two groups was separately measured. During the following eight days, mean daily consumption per locust was 160 mg. in Group B and only 100 mg. in Group A. From the 25th day, by which time all the males were mature, consumption in Group B also fell and it was then similar in both groups.

This early decline in feeding associated with early maturation was repeatedly observed but it was uncertain whether the decline was the cause or the result of maturation and it was also possible that the tendency to mature early was associated with an inherent tendency to low consumption. Any very large difference in early consumption between the two 5-male groups in Experiment IV would certainly have been observed, as was that which developed later. A smaller difference might, however, not have been noticed. In Experiment III, the weight of faeces expelled by each isolated male was recorded daily. Four of these males matured on or before the 18th day and three were still immature at the end of the fifth week. The mean weights of faeces per day expelled by these seven males during the first ten days of adult life were as follows:—

Early maturing — 71, 100, 124 and 143 mg.

Late maturing — 213, 213 and 177 mg.

The faeces were collected daily on eight occasions and after two days on one occasion. The mean figure for all four early-maturing males was always lower than that for the late-maturing ones; the difference between the two sets of observations was highly significant ($n=8$, $t=4.396$, $P<.01$). Feeding was here measured by excretion only, but the three late-maturing males increased their weight during the first ten days by 74, 67 and 68 per cent. while the four early-maturing ones increased weight by only 50, 48, 28 and 28 per cent. Mean weight at emergence was almost identical. There could thus be no doubt that the difference in excretion did reflect a difference in the quantities eaten rather than a difference in the proportion of the food utilised.

In this experiment, therefore, those isolated males which ate least matured earliest. This result, which is confirmed by experiments to be described later, gives further reason to doubt that the accelerating effect of crowding is directly attributable to its stimulating effect on feeding.

Casual observation revealed that the size of the faecal pellets was roughly proportional to the level of consumption at the period concerned. During the early period of maximum consumption, the pellets were much larger than they were after the level of feeding had declined. In Experiment IV, the pellets were both weighed and counted on several occasions. From the third to the eighth day the average weight of one pellet was 4.8 mg.; during the fourth week it was 3.1 mg. and during the fifth week 1.9 mg. There was no appreciable difference in pellet size between the crowded and isolated males except in so far as crowding was associated with earlier maturity and decline in the level of feeding. The pellets of the two 5-male groups and of the isolated males in Experiment IV were weighed and counted at the 23rd day. Those of the early-maturing group averaged 2.6 mg., those of the later-maturing group 4.0 mg. and those of the isolated males (only one of which was mature at this stage) 4.7 mg. By the fifth week, the pellets of both the 5-male groups (now all mature) were reduced to about 2 mg. while those of the five isolated males which were still immature were reduced only to 3.6 mg. This was the general pattern observed in all experiments, and decline in feeding associated with maturity or with advancing age could always be visually appreciated by inspection of the faeces.

It was noticed that newly passed faeces of crowded adults were wetter in appearance than those of the isolated ones. On two occasions faeces were collected at hourly intervals between 10 a.m. and 3 p.m. from all the cages in Experiment IV and their water content estimated. The mean water contents of the crowd faeces were 72 per cent. on the first occasion and 73 per cent. on the second; those of the solitary faeces were 56 and 55 per cent. The difference was not due to more rapid drying of the faeces of the isolated males; only five males were present in each crowd so that the quantity of wet faeces present in the cage at any one time was insufficient materially to affect air humidity. The grass becomes very dry during the night and little feeding occurs towards the end of the 24-hour period. Observations made in the morning, before putting fresh grass in the cages, showed that excretion is at a very low level at this time and that the water content of the faeces from both crowded and isolated locusts is very low and does not differ consistently. The locusts were fed between 10 and 11 a.m.; faecal water content rose to the highest level between one and two hours after feeding time and began to decline in the early afternoon as the grass began to become dry. The water content of faeces collected hourly from the locusts in Experiment IV during the course of one day is shown in Table II.

TABLE II.

Weight and water content of faeces expelled by 10 isolated males and by 2 groups of 5 males on the 14th day of adult life.

	Isolated males			Groups of 5 males		
Time	Total weight of faeces (mg.)		Water content (%)	Total weight of faeces (mg.)		Water content (%)
	Wet	Dry		Wet	Dry	
10-10.45 a.m.* ..	25	22	12	25	24	4
11-12 a.m.†	200	76	62	640	154	76
12-1 p.m.	558	208	63	1042	246	76
1-2 p.m.	450	184	59	728	216	70
2-3 p.m.	298	188	37	222	100	55
Total	1531	678	56	2657	740	72

* Before putting fresh grass in the cage.

(Faeces collected within one hour of expulsion; locusts fed at 10.45 a.m.)

These figures indicate that the excess water in the crowd faeces is not the result of the locusts having maintained a higher level of feeding during the night but that less water is extracted from the fresh grass eaten in the morning. The disparity in water content is out of proportion to the disparity in the total dry weight of faeces passed. The crowds passed 9 per cent. more faeces than the solitaires but the water content was 16 per cent. higher. Measurements made four days later, by which time the feeding of the crowd had declined, showed that the water content of the crowd faeces was still 18 per cent. higher than that of the isolated males although the total dry weight of faeces passed during the observation period was actually lower by 14 per cent. It seems, therefore, that the difference is not entirely due to the food passing more quickly through the alimentary tract but that less water is extracted from it in a given time.

TABLE III.

Feeding, excretion and maturation of isolated and paired adult males during the first 20 days after emergence. (Dry weights of food eaten and of faeces excreted.)

	Experiment V				Experiment VI				Experiment VII			
	1st to 10th		11th to 20th		1st to 10th		11th to 20th		1st to 10th		11th to 20th	
	2	1	2	1	2	1	2	1	2	1	2	1
Days												
Density												
mg. eaten per locust per day	..	343	285	265	237	231	162	167	280	210	243	208
mg. excreted per locust per day	..	195	198	196	127	120	118	119	160	123	156	133
Utilisation (%)	..	43	31	26	46	48	26	29	43	41	36	36
Percentage mature on last day	..	0	0	0	0	0	90	60	0	0	10	50

Just as the size of the faecal pellets declines with age and maturity so also does their maximum water content. During the fourth week of adult life the water content of faeces passed between 12 and 1 p.m. varied from 43 to 59 per cent. for the crowds and from 21 to 59 per cent. for the isolated males. Figures of over 60 and 70 per cent., such as were recorded during the first three weeks, were not reached. In Experiment IV, early decline in water content associated with early maturity was seen in the earlier maturing of the two 5-male groups, Group A. Faeces were collected from both groups within an hour of expulsion on the 18th, 21st and 22nd days. The water contents of the faeces from Group A on the three days averaged, respectively, 67, 31 and 18 per cent.; those from Group B, none of which was mature till the 23rd day, averaged 75, 43 and 49 per cent.

Young males in pairs and isolated.

In the last section it was shown that low-density crowding of five males in a 9-litre cage was sufficient to increase the quantity of food eaten during early adult life. Pairs of males tend to mature more rapidly than single males (Norris, 1954), and Hunter-Jones (1958) showed that some of the effects of crowding occur when hoppers are kept in single pairs and when females are paired with single males. The experiments described in this section were designed to show whether feeding is mutually affected when two males only are present.

Three experiments, numbers V, VI and VII, were carried out, in each of which the feeding and excretion of ten isolated males was compared with that of five pairs of males from the same batch. The results are summarised in Table III, and those for Experiment VII are shown graphically in fig. 2.

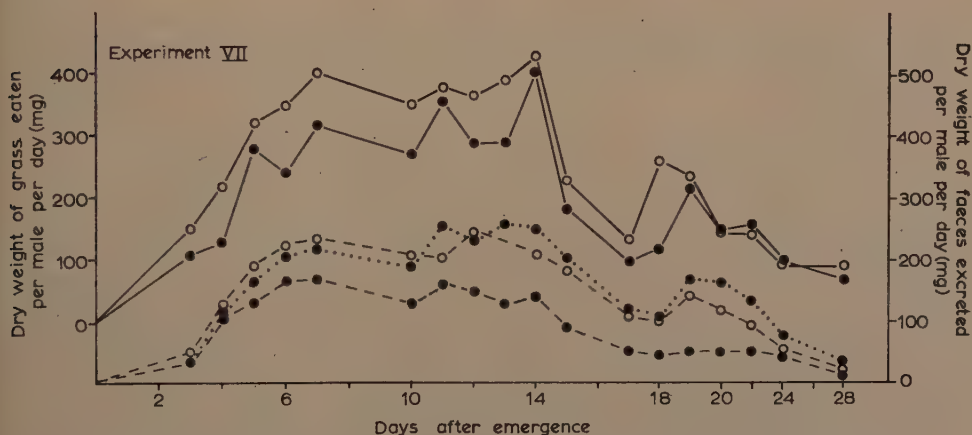


Fig. 2.—Mean daily dry weights of grass eaten and faeces excreted per adult by pairs of males and by isolated males. Faeces of early- and late-maturing isolated males separately recorded. (Experiment VII.)

Pairs of males, o; isolated males, ●; grass eaten, —; faeces excreted, ---- (pairs and early-maturing isolated), and (late-maturing isolated).

In Experiments V, VI and VII, the paired males ate 10, 3 and 33 per cent., respectively, more than the isolated ones during the first ten days of adult life. In the three experiments together, a total of 14 observations were made during the first ten days and with one exception in Experiment VI the paired males had eaten more than the isolated ones during all the 2-or 3-day periods concerned. The ratios of the quantities eaten by the two sets of males at each observation

differed significantly from one ($n=13$, $t=4.407$, $P<0.001$). At all 14 observations the pairs excreted more than the isolated males and again the ratios differed significantly from one ($n=13$, $t=5.4427$, $P<0.001$). The excess feeding by the pairs was very small indeed in Experiment VI and this was probably related to unusually early decline in feeding associated with extremely early maturation. Six of the paired males were mature by 14 days and all by 17 days. None of the isolated males was mature by 14 days and only half of them by 17 days. In Experiment VII on the other hand, in which excess feeding by the pairs was greatest, maturation was actually earlier in the isolated males, five of the latter and only one of the former being mature by three weeks. Both in Experiment V and in Experiment VII, excess feeding by the pairs was continued up to the end of the third week, and in each experiment taken separately the differences for the whole period were highly significant (Expt. V: $n=8$, $t=4.831$, $P<0.01$. Expt. VII: $n=11$, $t=6.559$, $P<0.001$).

It is noticeable that consumption by the pairs was highest in Experiment V where maturation was slowest and lowest in Experiment VI where it was most rapid (see Table III). The locusts in Experiment VI emerged in February at a time when the grass had been spoilt by frost and was brown and limp. Here again, therefore, there is a strong indication that a low level of feeding is associated with early maturation and, at least in this experiment, this was in turn associated with unpalatable food.

In Experiments VI and VII, the dry weights of faeces excreted by each isolated male were separately recorded so that the feeding rates of early- and late-maturing males could be compared. In Experiment VII, five of the males became mature from the 14th to the 17th day and the remaining five were still immature at 28 days; there was therefore a clear-cut division between early and late maturers which provided excellent material for this comparison. Separate records were made from the third day onwards (see fig. 2). Between the fourth and the eleventh day (by which time the early-maturing males were approaching maturity), the mean daily excretion of each of the ten individuals was as follows:—

5 early-maturing males: 113, 123, 149, 152, 177 mg. (mean 143 mg.)

5 late-maturing males: 171, 175, 194, 221, 246 mg. (mean 201 mg.)

With one exception, all the early-maturing males excreted less than the late-maturing ones and the difference between the means of 143 and 201 mg. was significant ($n=8$, $t=3.188$, $P<0.02>0.01$). During this period, five collections of faeces were made, and the mean weight of faeces excreted by all five early-maturing males in the period since the preceding collection can be compared with that excreted by all five late-maturing ones. The figures are shown in Table IV. At every observation the mean weight excreted by the late-maturing ones was very considerably larger. The differences between the two sets of figures differed significantly from zero ($n=4$, $t=5.535$, $P<0.01$).

While there was no significant difference in emergence weight between the two sets of males, the late-maturing ones increased weight during the first ten days by 51 per cent. and the early-maturing ones by only 41 per cent. There is, therefore, no reason to suppose that the greater excretion of the late maturers is due to a lower rate of utilisation rather than to a higher level of feeding.

In Experiment VI, there were five isolated males which matured between 15 and 17 days and four males still immature at 24 days. Mean daily excretion of these nine individuals from the second to the tenth day was as follows:—

5 early-maturing males: 87, 92, 113, 113, 123 mg. (mean 106 mg.)

4 late-maturing males: 109, 110, 146, 163 mg. (mean 132 mg.)

In this case there was some overlapping in the figures; the difference was not statistically significant but it was in the same direction as in Experiment VII

and at all four collections made during the period more had been excreted by the late than by the early maturers. Early and late maturers increased in weight during the first 14 days by 50 and 62 per cent., respectively, the difference again being in the same direction as in Experiment VII.

Utilisation varied from 41 to 48 per cent. during the first ten days and from 26 to 36 per cent. from the tenth to the twentieth day. As in Experiments I to IV, utilisation was lower in the later period and there were no significant differences between the treatments in this respect.

TABLE IV.

Mean daily weight (in mg.) of dry faeces excreted by 5 early- and 5 late-maturing isolated males between the 4th and 11th days of adult life.

Day	Early-maturing	Late-maturing
4 to 5	131	166
5 to 6	166	206
6 to 7	167	221
7 to 10	126	187
10 to 11	162	254

Mutual effects on the water content of the faeces were well marked, the faeces of the paired males being obviously wetter than those of the isolated ones. In Experiment V, faeces passed during the preceding 5 or 6 hours (after the morning feed) were collected at 4 p.m. on four days and the water content estimated. The result was as follows:—

	Day 5	Day 9	Day 12	Day 14
Pairs:	55%	25%	18%	33%
Isolated:	18%	13%	9%	9%

In Experiments VI and VII, faeces were in each case collected on two occasions within an hour of being passed and their water content estimated. The results were as follows:—

	Day 3	Day 8	Day 10	Day 14
Pairs:	36%	38%	46%	46%
Isolated:	24%	30%	24%	17%
	Expt. VI		Expt. VII	

Although both the absolute and the relative figures for the two treatments are highly variable the faeces of the pairs consistently had a higher water content than those of the isolated males.

The above results show that the presence of one other locust in a nine-litre cage is sufficient to induce well-marked crowding effects on consumption and excretion.

Young males in pairs with each other and in pairs with mature males.

It was shown (Norris, 1954) that newly-emerged males kept in pairs with single mature males became mature more rapidly than those kept in complete

isolation or in pairs with single immature males or females. It has been shown above that the accelerating effects of crowding on maturation are associated with increased feeding during early adult life and that even the presence of one other male in the cage increases feeding to a marked degree. The two experiments, numbers VIII and IX, described in this section were designed to show whether young males and mature males have different effects on feeding.

In each experiment the feeding of ten newly emerged males kept in pairs with each other was compared with that of ten newly emerged males from the same batch each kept with one fully mature yellow male. In Experiment VIII, there was also a third series of newly-emerged males kept in complete isolation. A comparison between these and the pairs of young males has already been made in the last section under Experiment VI (see Table III). In order to estimate the quantities eaten by the males kept with mature males it was necessary to subtract from the totals the small amounts eaten by the mature males. This was done by estimating the amounts eaten by ten other mature males taken from the same batch and kept in pairs. The abdomens of the mature males were enclosed in thin rubber sacs so that their faeces were separable from those passed by their immature companions. Enclosure of the abdomen in a rubber sac does not impair the accelerating effect of the mature male (Norris, 1954).

The results of these two experiments are summarised in Table V, and those of Experiment IX are shown graphically in fig. 3. In Experiment VIII, the

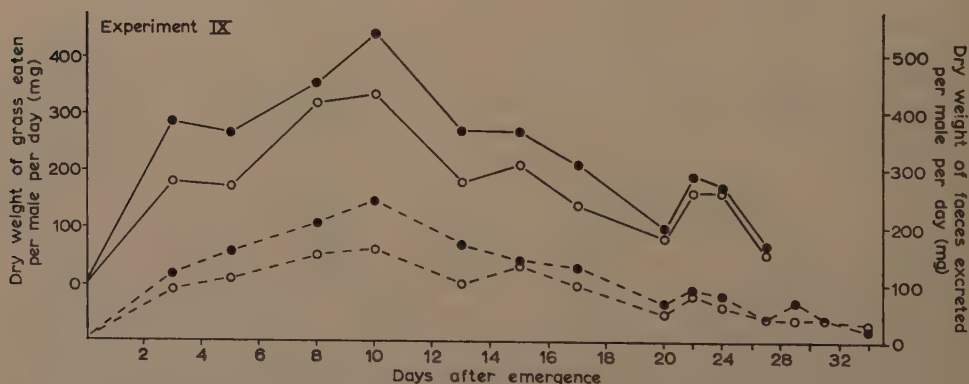


Fig. 3.—Mean daily dry weights of grass eaten and of faeces excreted per adult by pairs of young males and by young males kept in pairs with mature males. (Experiment IX.)

Pairs of young males, ●; young males in pairs with mature males, ○; grass eaten, —; faeces excreted, ----.

young males kept in pairs with each other ate 43 per cent. and excreted 53 per cent. more during the first ten days than those kept in pairs with mature males. Four observations were made during this period, and the males paired with each other had eaten and excreted more on each occasion. The differences between the four pairs of figures differed significantly from zero (Consumption: $n=3$, $t=9.705$, $P<.01$. Excretion: $n=3$, $t=5.146$, $P<.02>.01$).

In Experiment VIII, the isolated males, which ate only slightly less than those kept in pairs (see Expt. VI, Table III) also ate 39 per cent. and excreted 45 per cent. more than those paired with mature males. The difference between the isolated and paired males in this experiment was, however, much less than

in the other two experiments in which this comparison was made (Expts. V and VII, Table III), and it is therefore possible that the consumption of isolated males might not always so greatly exceed that of those paired with mature males. Further evidence is required on this point. It was not possible to separate the faeces of two young males kept together, but the total amounts excreted by each individual isolated male and each male with a mature male were separately estimated at each of the four collections made during the first ten days. This gave a total of 40 figures for each treatment. The difference between the means of 266 mg. for the isolated males and 188 mg. for the males with mature males was very highly significant ($n=78$, $t=3.991$, $P<.001$).

TABLE V.

Feeding, excretion and maturation of young males in pairs with males of their own age (A) and with mature males (B). (Dry weights of food eaten and of faeces excreted.)

Experiment	VIII				IX			
Days	1st to 10th		11th to 20th		1st to 10th		11th to 20th	
Grouping	A	B	A	B	A	B	A	B
mg. eaten per locust per day	237	166	162	164	325	235	170	148
mg. excreted per locust per day	127	83	118	111	178	125	103	92
Utilisation (%)	46	50	26	32	45	47	39	38
Percentage mature on 14th day	—	—	30	60	—	—	0	30

During the first 14 days, the isolated males and the young males kept in pairs increased their weight by 58 and 55 per cent. and those paired with mature males by 46 per cent. There was no further weight increase in any treatment by the end of the fifth week.

The average maturation time of the young males kept in pairs was 17.1 days; they matured between the 14th and the 24th days. The average maturation time of the males kept in pairs with mature males was 14 days; six were mature by the 14th day, and the last by the 17th day. During the third week, when the pairs of young males were maturing, their feeding fell rapidly to a level even slightly lower than that of those kept with mature males. Maturation of the pairs in this experiment was so rapid that the accelerating effect of the mature males was necessarily small.

In Experiment IX (fig. 3), the young males kept in pairs ate 38 per cent. and excreted 42 per cent. more during the first ten days than those kept in pairs with mature males. At all four observations made during this period the difference was in the same direction, and the differences between the four pairs of figures differed significantly from zero (Consumption: $n=3$, $t=3.731$, $P<.05>.01$. Excretion: $n=3$, $t=5.555$, $P<.02>.01$). The males paired with each other gained weight by 65 per cent. during the first 14 days and became mature between the 17th and the 41st day; the mean maturation time was 26 days. The males kept with mature males gained weight by only 47 per cent. in the first 14 days, by which time three of them were mature; the last one matured at 31 days and the mean maturation time was 17 days. Maturation of the young

pairs in this experiment was much slower than in the previous one and they continued to eat more than those kept in pairs with mature males during the third and fourth weeks.

In neither experiment did the weight of the males kept with mature males catch up with that of the others. Their weight appears to become stabilised at or before the time of maturation and when weighed at the age of five or six weeks (when all were mature) they were no heavier than they were at 14 days.

In neither of these two experiments was there any appreciable effect of the treatment on the proportions of food utilised.

In the previous experiments on the effects of crowding, it was noted that the faecal pellets excreted by the crowded and isolated locusts did not at first differ in size although the decline in size which is associated with maturity naturally occurred earlier in the crowded locusts. In both Experiments VIII and IX, however, faecal size was from the beginning considerably reduced as a result of a young male being kept with one mature male. The dry weight of a single pellet at various stages in the two experiments is shown in Table VI.

TABLE VI.

Average dry weights (mg.) of single faecal pellets excreted by young males kept in pairs with each other (A) and in pairs with mature males (B).

Experiment	Days	A	B
VIII ..	3rd to 5th	4.3	3.5
	6th to 7th	5.3	4.2
IX ..	4th to 6th	4.5	3.6
	7th to 8th	4.8	3.8
	9th to 10th	5.3	3.4

In Experiment VIII, faecal water content was only recorded during one day; it was 38 per cent. for the males kept with each other and 27 per cent. for those kept with mature males. In Experiment IX, estimations of water content were made on five days between the third and the fourteenth day. The faeces were collected on each day between the hours of 12 noon and 1 p.m. when water content is near the maximum. The following pairs of figures, of which the first refers to the young males kept in pairs and the second to the young males kept with mature males, show the difference in water content:—

Day 3, 54-42%.	Day 6, 43-30%.	Day 7, 65-30%.
Day 10, 55-52%.	Day 14, 65-46%.	

The faecal water content of the males kept with mature males was consistently lower than that of the others. It was shown that confinement of a young male with another young male increases faecal water content as compared with isolation, but it seems that confinement with a mature male has less effect or, since low consumption is in general associated with low water content, more probably reduces it. Since no comparison was made with isolated males in this experiment, this point remains uncertain.

Mature males crowded and isolated.

In males over four weeks old, whether crowded or isolated, feeding is usually reduced to a low level. The average dry weight of food eaten daily was usually

between 50 and 100 mg. There is considerable individual variation in the age at which this basic level is reached, but once established it is maintained, with fluctuations, for the remainder of life. Although no continuous upward or downward trends were discerned during this period, the fluctuations may be quite large, and a sharp change in the level may occur quite suddenly and be sustained for some days in the absence of any apparent change in the environment. These fluctuations are most probably due to changes in the nature of the grass, the one uncontrolled factor. Species, water content and state of growth may all be concerned.

In those experiments, in which the feeding of crowded and isolated males was compared, it was found that although the crowded ones ate more during the first ten days of adult life, the earlier onset of maturity was associated with a more rapid fall in consumption, so that for a short period they ate less than the isolated ones. When the isolated ones, in their turn, became mature, their feeding again dropped slightly below that of the crowded ones (see fig. 1). The difference, however, was very small, only a matter of about 25 mg. per locust per day, and as the observations were not in most cases long continued there was some doubt as to its significance. Further experiments were therefore carried out in which the feeding of the same mature males kept crowded and isolated was observed. Owing to the smallness of the absolute quantities eaten at this stage it seemed doubtful if differences in the rates of feeding could be sufficiently accurately measured by the methods used, particularly when the number of individuals was small. In most cases, therefore, relative levels of feeding were estimated by comparing the rates of excretion, which could be accurately measured. Because of the fluctuations which occur it was always necessary, when assessing the effects of a change in grouping, to compare the locusts with others not subjected to change or subjected to change in the opposite direction.

Experiment X.—Two sets of ten mature males, all aged 30 days at the beginning of the experiment, were compared. For the first week, set A was isolated and set B crowded. During the second week, grouping was reversed, set A being crowded and set B isolated. Average weights of faeces excreted per locust per day were as follows:—

1st week		2nd week	
A (isolated)	34 mg.	A (crowded)	52 mg.
B (crowded)	46 mg.	B (isolated)	39 mg.

During both weeks, those males that were crowded excreted more than those that were isolated, and each set of males also ate more when crowded than when isolated. There was, however, an over-all rise in excretion affecting both treatments during the second week and this resulted in the rise in set A being much greater than the fall in set B.

Experiment XI.—Three sets of ten mature males aged four weeks at the beginning of the experiment were compared for two weeks. During the first week, sets A and B were all kept in isolation and set C was kept in pairs. During the second week, set A was crowded ten per cage, set C was isolated, and set B remained in isolation. Average weights of faeces excreted per locust per day were as follows:—

1st week		2nd week	
A (isolated)	32 mg.	A (crowded)	41 mg.
B "	43 mg.	B (isolated)	41 mg.
C (in pairs)	48 mg.	C "	37 mg.

During the second week, the level of excretion rose by about 22 per cent. in set A which was crowded after isolation, decreased by about the same amount in set C which was isolated after being paired, and remained almost the same in set B, which was unchanged.

Experiment XII.—Sixteen mature males aged six weeks and hitherto kept in pairs were divided into two sets, A and B. During the first week, set A were isolated and set B crowded eight in a cage. During the second week, grouping was reversed, and during the third week both sets were crowded. Each set was therefore crowded for two weeks and isolated for one week. The weights of faeces excreted per locust per day were as follows:—

1st week		2nd week		3rd week	
A (isolated)	46 mg.	A (crowded)	56 mg.	A (crowded)	58 mg.
B (crowded)	63 mg.	B (isolated)	54 mg.	B (crowded)	67 mg.

Inspection of these figures shows that, density apart, excretion was consistently slightly higher in set B than in set A, but in both sets it was lower by about 20 per cent. when kept in isolation.

In all the above experiments, crowding resulted in a slight rise in the level of excretion and, by inference, of feeding. The difference, however, was small and within the limits of individual variation, at least when working with comparatively small numbers of locusts; it was only demonstrated by subjecting the same individuals to crowding after isolation or *vice versa*. It is arguable that the changes in themselves may have affected feeding, but the result is supported by the observations made on mature males which had been kept continuously crowded or isolated from emergence (Experiments I to IV).

Late-maturing immature males isolated and kept in pairs with mature males.

Although the initial period of heavy feeding tends to be prolonged in late-maturing males, their consumption usually falls to a low level during the fourth or fifth week from emergence, by which time it may be little or no higher than that of mature males from the same batch. Later on, as the period of immaturity continues, a very low level may be maintained. Members of the same batch may exhibit great variability in the age at which feeding reaches the minimum level. The excretion of three immature males eight weeks old was recorded for a period of six days. Average daily excretion in two of the males had reached the very low levels of 15 and 18 mg., and the average weights of single faecal pellets were, respectively, 1.4 and 2.0 mg. The third male excreted an average of 62 mg. and the pellets averaged 4.3 mg. Excretion, and by inference consumption, was therefore about four times greater in the case of the last-mentioned individual than in the other two. The previous history of all these males was identical and they were very similar in appearance, having the dark brownish-red coloration typical of males showing delayed maturation in this laboratory. They showed no visible signs of approaching maturity.

It has been shown that the accelerated maturation which occurs in young males kept from emergence with mature males is associated with a reduced rate of feeding. It seemed desirable to know if any change occurs in the feeding of older immature males when maturation is suddenly stimulated by the introduction of a mature male. Because of the considerable fluctuations in the level of feeding which occur independently of density changes it was always necessary to compare the males subjected to change with others remaining unchanged. Excretion only was measured and the abdomen of the mature male introduced was enclosed in a rubber sac so that this could be done accurately.

Experiment XIII.—Two of the immature males eight weeks old mentioned above were used in this experiment. A mature male was put into the cage containing the male which had excreted an average of 15 mg. during the preceding six days. For the next three days, excretion averaged 40 mg. and by the fourth day the male was mature. During the same period, excretion in the second male, which had excreted an average of 62 mg. in the previous six days (and was still in isolation), rose to 140 mg. Excretion had therefore more than doubled in

both males, although one had become mature and the other remained immature. A mature male was then put in the cage with the second male. During the next three days, excretion by the second male fell again to 52 mg. and it was mature by the fourth day. During this period, excretion in the first male also fell to 31 mg. There is no evidence here that the introduction of the mature male had any effect on the level of feeding; one male became mature on a rising and the other on a falling level. These figures provide, incidentally, a good example not only of great individual variation exhibited by isolated males in identical conditions but also of the immense fluctuations which occur in the same individual from one period to another.

Experiment XIV.—Eight isolated immature males four weeks old were divided into two sets, A and B. The excretion of these males was recorded separately for two 2-day periods. During the first period, all the males were kept in isolation; during the second, one mature male was put into each of the cages of set A. Average weights of faeces excreted daily by each of the eight males was as follows:—

First period	A (isolated) 134, 72, 65, 56 (mean 82 mg.)
	B (,) 97, 56, 32, 18 (mean 51 mg.)
Second period	A (with mature male) 82, 28, 23, 36 (mean 42 mg.)
	B (isolated) 93, 34, 25, 21 (mean 43 mg.)

During the first period, when all the males were isolated, excretion was much greater in set A than in set B; during the second, excretion in set A, put with mature males, fell by nearly 50 per cent., the figures for the individual males being 38, 61, 65 and 36 per cent. In set B, which remained in isolation, excretion fell on the average by only 16 per cent., the figures for the individual males being 4, 39, 22 and 14 per cent. There is certainly a suggestion here that the introduction of the mature males induced a larger decrease in feeding. The numbers of individuals were too small for the difference to be statistically significant but at least it can be said that the mature male had not stimulated feeding.

Experiment XV.—The excretion of six isolated males which were still immature at the age of 12 weeks was first compared with that of six others from the same batch which had very recently become mature. The faeces of each male were separately recorded. During the course of a week, average daily excretion per immature male was 20.5 mg. (range 14 to 29 mg.) and excretion per mature male was 19.5 mg. (range 15 to 22 mg.). There was, therefore, no significant difference between the two sets of males, in both of which excretion was at a very low level. At the end of this week a mature male was put into each of the cages with the immature males. Four of them became mature within four days and the last two by the sixth day. During this week, their average daily excretion was 26 mg. (range 19 to 32 mg.); that of the mature males, still isolated, was 23 mg. (range 16 to 37 mg.). With the exception of two individuals, one in each set, excretion was slightly greater during this week than during the previous one but there was still no significant difference between the two sets. In this experiment, no effect of the mature male on feeding was demonstrated and maturation occurred without any change not shared by the control males.

Owing to the difficulty of obtaining many old immature males at the same time, the only data available as to the effects of mature males on their feeding are those from the last three experiments. The results are inconclusive, but it is considered that any marked and consistent effect on feeding would have been revealed, and it is also evident that belated maturation may occur either during periods of rising or falling excretion. This does not suggest that it occurs as a result of any interference with the feeding regime.

Late- and early-maturing mature males in similar groups.

While Experiment XV was in progress, a set of eight isolated mature males from a later batch was also under observation. These males were six weeks old and had matured early at the age of three weeks. Their excretion was compared with that of the six mature control males which were 12 weeks old and had only recently become mature. The average daily excretion of the eight early-maturing males was 40 mg. during the first week and 50 mg. during the second week. It was, therefore, twice as great as that of the six late-maturing ones (19.5 mg. during the first week and 23 mg. during the second week).

For the next ten days after the end of Experiment XV six of the early-maturing males were crowded in one cage and compared with the six of the late-maturing ones, also crowded. Average daily excretion per male was 54 mg. for the early-maturing ones and 30 mg. for the late-maturing ones; the average weight of a single faecal pellet was, respectively, 2.8 and 1.8 mg. Although, therefore, the males were all in identical conditions and fed on the same grass, excretion, and by inference feeding, was consistently maintained at a higher level in the early-maturing males. The late-maturing males had been, on the average, slightly lighter at emergence than the others (1.345 g. as compared with 1.467 g.) but owing to their initial weight increase having been greater they were at this time much heavier than the early-maturing ones (2.339 g. as compared with 2.066 g.). As previously recorded (p. 746) the initial weight increase of late-maturing males tends to continue for a longer period than that of very early-maturing ones in which it is cut short at the time of maturation.

At the end of the experiment, all the locusts were killed and estimations made of their water content. This was found to be much higher in the early- than in the late-maturing males; in the former it ranged from 61.8 to 68.6 per cent. (mean 63.6%) and in the latter from 48.8 to 57 per cent. (mean 53.6%). The difference was clearly related to the difference in the level of feeding, and it is probable that this was in turn related to the difference in maturation time. Experiments carried out in this laboratory by Mr. G. G. Cavanagh (unpublished) have shown that water content falls to a low level in late-maturing males and rises only very slowly after maturation.

Discussion.

The experiments described in the preceding pages have shown that crowded males eat and excrete more during the early days of adult life than isolated ones and that mutual crowding effects occur when only two males are present in a 9-litre cage. This might suggest that the accelerated maturation which occurs when the locusts are crowded is the result of increased feeding. Against this, however, it has been shown that young males kept in pairs with mature males (a treatment which accelerates maturation) eat and excrete *less* during early adult life than those kept in isolation or in pairs with other young males. In this case accelerated maturation is associated with decreased feeding.

Maturation puts an end to the period of active feeding and rapid increase in weight which occurs during early adult life, and those males that mature very early remain permanently lighter than those that mature later and in which the period of active feeding is prolonged. Mr. Cavanagh (unpublished) has shown that the fat content of late-maturing males continues to increase beyond the point reached in earlier-maturing ones, the increasing fat content being associated with decreasing water content. It is uncertain whether the decline in feeding which occurs near the time of maturation is the cause or the result of maturation. Since, in the very earliest-maturing males, maturation may first precede the decline, it is perhaps more likely that the level of feeding is depressed by the physiological changes which occur at maturation. When all males are kept in isolation there is a marked tendency for those individuals which excrete least from the outset of

adult life to mature earliest; since their body-weight also increases less it may be presumed that a lower rate of excretion does reflect a lower rate of feeding. These observations are compatible with those previously made on seasonal differences in maturation time (Norris, 1957). Maturation of isolated pairs of adults in the laboratory is more rapid during the winter than during the summer months. The highest incidence of delayed maturation occurs among adults emerging in April-May and in September when the grass is young and succulent; the most rapid maturation occurs in late winter when the grass is often spoilt by frosts and of very poor quality. It was shown that the broad seasonal difference was attributable to day length, and that the long summer days, which stimulated feeding, tended to prolong maturation time, but it seemed probable that the quality of the grass had effects additive to those of photoperiod at the peak periods for rapid and slow maturation. It appears that, given a minimum necessary diet, any factor which reduces the level of feeding and retards the building-up of fat reserves tends to accelerate maturation. Such factors include short photoperiod, poor-quality grass, constitutional tendency to low consumption and the presence of a mature male. This is by no means surprising if the delays in maturation are regarded as having the nature of diapause. The building-up of large fat reserves accompanied by reduction of water content is a characteristic feature of the onset of diapause.

In view of the above conclusions it seems anomalous that crowding, which accelerates maturation, should also increase the level of feeding. While it is possible that other factors are concerned in these conditions, it is very probable that the extra food eaten is insufficient to compensate for greater metabolic requirements and that the crowded locusts are in fact less well able to build up their food reserves than the isolated ones. It was noticeable that in two out of four experiments the rate of weight increase of the crowded males during early adult life was actually slightly lower than that of the isolated ones. In one of these experiments the excess feeding by the crowded ones was at a maximum. In view of all the other observations which converge to establish an association between a low level of feeding and rapid maturation it can at least be said with confidence that the earlier maturation of the crowded locusts cannot be due to their higher consumption. It should be remarked, however, that very different results might be obtained were the locusts fed on a nutritively less adequate diet than grass or kept in a physical environment less favourable to rapid maturation.

Summary.

It has previously been shown that the sexual maturation of males of *Schistocerca gregaria* (Forsk.) is accelerated by crowding with other individuals of similar or greater age, and that the maturation of males kept in single pairs with older mature males is accelerated as compared with that of isolated males or males kept in single pairs with other young males or females of their own age. The effects of these groupings on the levels of feeding and excretion are investigated in the present work.

Crowded males ate and excreted more than isolated ones during the first ten days of adult life. Five males in a 9-litre cage are sufficient to induce almost the full effect of crowding, and marked effects are shown when only two males are present in such a cage.

After the second or third week, the level of feeding declines. This occurs earlier in early-maturing individuals, so that for a short period the crowded males eat little more or even less than the isolated ones. When the isolated males in their turn become mature their feeding again falls slightly below that of the crowded ones. When all males are isolated, there is a significant tendency for

those males which eat least from the beginning of adult life and which increase their weight least to become mature earliest.

The proportion of the food utilised was not affected by density. It was higher during the early period of maximum consumption than it was after the level of feeding declined.

The size of the faecal pellets declines with the level of feeding but is not otherwise affected by density.

The faecal pellets of the crowded males and of males kept in pairs have a higher water content than those of isolated ones. This is not entirely due to more rapid passage of the food through the alimentary canal. Water content declines with the level of feeding. This is true whether the decline in feeding is the diurnal one due to drying out of the grass or the permanent one which occurs as the locusts grow older.

Young males kept in pairs with mature males eat and excrete less during the first ten days of adult life than those isolated or kept in pairs with other young males. They increase weight less rapidly, become mature at a lower weight and remain permanently lighter than the others. Their faecal pellets are smaller and have a lower water content than those of the pairs of young males.

The level of excretion (and by inference of feeding) in older mature males is slightly increased by crowding.

In older isolated males showing delayed maturation, excretion (and by inference, feeding) is usually reduced to a very low level. When maturation was stimulated by the introduction of a mature male no consistent effects on feeding were demonstrated. Maturation sometimes occurred during a period of rising consumption and sometimes during one of falling consumption.

Mature males which had become mature early and others which had matured late were simultaneously observed at the same densities. The early-maturing males, although lighter in weight relative to their emergence weight, excreted (and, by inference, ate) more than the late-maturing ones and had a higher percentage water content.

The results in general point to an association between a low level of feeding and rapid maturation and it is concluded that the earlier maturation of crowded males must either be independent of the level of feeding or be due to their extra consumption being insufficient to compensate for greater metabolic requirements.

Acknowledgements.

I am indebted to the staff of the Anti-Locust Research Centre for help of many kinds and particularly to Miss P. Miller (now Mrs. Nisbett) who was responsible for most of the routine work and to Mr. D. E. Davies for help with statistics.

References.

- ASKET SINGH (1957). Some critical observations on the feeding activity of the desert locust, *Schistocerca gregaria* (Forskål), under different environmental conditions.—*Res. Bull. Panjab Univ. Zool.* no. 108 pp. 291–298.
- CHAUVIN, R. (1941). Contribution à l'étude physiologique du criquet pèlerin et du déterminisme des phénomènes grégaires.—*Ann. Soc. ent. Fr.* **110** pp. 133–272.
- DAVEY, P. M. (1954). Quantities of food eaten by the desert locust, *Schistocerca gregaria* (Forsk.), in relation to growth.—*Bull. ent. Res.* **45** pp. 539–551.
- HUNTER-JONES, P. (1958). Laboratory studies on the inheritance of phase characters in locusts.—*Anti-Locust Bull.* no. 29, 32 pp.

- NORRIS, M. J. (1952). Reproduction in the desert locust (*Schistocerca gregaria* Forsk.) in relation to density and phase.—*Anti-Locust Bull.* no. 13, 49 pp.
- NORRIS, M. J. (1954). Sexual maturation in the desert locust (*Schistocerca gregaria* Forskål) with special reference to the effects of grouping.—*Anti-Locust Bull.* no. 18, 44 pp.
- NORRIS, M. J. (1957). Factors affecting the rate of sexual maturation of the desert locust (*Schistocerca gregaria* Forskål) in the laboratory.—*Anti-Locust Bull.* no. 28, 26 pp.
- WEIS-FOGH, T. (1952). Fat combustion and metabolic rate of flying locusts (*Schistocerca gregaria* Forskål).—*Phil. Trans. (B)* **237** pp. 1–36.

ACARICIDE RESISTANCE IN THE RED TICK, *RHIPICEPHALUS EVERTSI* NEUMANN.

By G. B. WHITEHEAD * and J. A. F. BAKER.†

L.P.

Resistance to a variety of insecticides‡ in populations of ticks has been observed in several parts of the world. With the exception of resistance to chlordane in the 'three-host' dog tick, *Rhipicephalus sanguineus* (Latr.), in North America (Hansens, 1956), resistant populations appear to have developed only in the 'one-host' ticks of the genus *Boophilus* in Africa, Australia and South America.

In South Africa, the development of resistance to sodium arsenite, γ BHC and related chlorinated cyclic hydrocarbon insecticides and DDT has been observed in the blue tick, *Boophilus decoloratus* (Koch), but no increased tolerance to insecticides has been observed in other species of ticks against which regular control measures are directed.

Early in 1959, field observation on the farm Tayside, in the East London district (South Africa), indicated that the control of the red tick, *Rhipicephalus evertsi* Neum., a 'two-host' tick, by a practice of dipping in a recommended concentration of toxaphene was not consistent with previous experience. It was established chemically that the concentration of toxaphene in the dip was up to strength (0.25%) and the possibility of resistance to toxaphene in the population of *R. evertsi* on this farm was suspected.

These observations initiated both field and laboratory investigations designed to detect insecticide resistance in the Tayside population of the tick by comparison with populations from other sources.

Field investigations.

Hand spraying: Tayside.

A group of four head of cattle was sprayed with a mechanical spray pump on four successive occasions at seven-day intervals with a preparation of 0.25 per cent. toxaphene. After the fourth application, the concentration of the spray wash was increased to 0.5 per cent. toxaphene and applications continued for a further four weeks. The effect of treatment was assessed by making counts of adults of *R. evertsi* in the peri-anal region and larvae and nymphs on the inner surface of the ears immediately prior to each weekly application. Counts were also made of larvae, nymphs and adults on a group of four animals which was left untreated for the full seven weeks of the trial. The results of this trial are presented in Table I.

These results showed that toxaphene sprays at a concentration of 0.25 per cent. had little effect on the immature and adult stages of *R. evertsi* on the farm Tayside. Toxaphene at 0.5 per cent. appeared to show some degree of control of adults, larvae and nymphs but was considerably less effective than might have been expected from previous experience of the effectiveness of toxaphene on the red tick.

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‡ In view of the fact that all the substances tested were originally developed as insecticides, this term has been used throughout the paper in preference to "acaricide."

Hand dressing: Tayside and Riverdale.

The initial trial at Tayside indicated that the populations of *R. evertsi* from this locality were showing an increase in tolerance to toxaphene, and in order to establish this fact a hand-dressing trial with a number of insecticides was initiated.

TABLE I.

Assessment of larval and nymphal populations and counts of adults of *R. evertsi* from toxaphene-treated and untreated cattle on the farm Tayside.

Date of application	Untreated (average from four head)			0.25% toxaphene treatment (average from four head)		
	Larvae	Nymphs	Adults	Larvae	Nymphs	Adults
24.iv.59	+++	+++	22.5	+++	+++	23.75
30.iv.59	+++	+++	31.75	+++	+++	24.0
7.v.59	+++	+++	43.5	+++	+++	17.75
14.v.59	+++	+++	40.5	+++	+++	25.25
0.5% toxaphene treatment (average from four head)						
21.v.59	+++	+++	40.0	+++	+++	21.75
28.v.59	+++	+++	46.5	+++	+++	16.75
4.vi.59	+++	+++	36.75	+++	++	21.75
11.vi.59	+++	+++	30.75	++	++	12.25

+ = 0—25 approx.
 ++ = 25—60 "
 +++ = 60—600 "

At the same time a similar trial was conducted on the farm Riverdale, where toxaphene at the normal field recommendation of 0.25 per cent. was considered still to be giving satisfactory control of infestations of *R. evertsi*.

At these two sites the insecticide dilutions were applied by hand to the inner and outer surfaces of the ears and to the peri-anal area with a sponge of synthetic material. Infested cattle were divided into groups of three head each at the Tayside site and two head each at the Riverdale site. The experimental cattle were treated at weekly intervals on five occasions at Tayside and four occasions at Riverdale. Apart from the hand treatment of ears and anal area no other treatment was applied. Results were assessed in a manner similar to the hand-spraying trial and are presented in Table II.

The effect of sodium arsenite on Riverdale and Tayside ticks was similar. At a concentration of 0.16 per cent. As_2O_3 , weekly treatments of sodium arsenite considerably reduced larvae, nymphs and adults after three and four weeks, respectively. It is concluded that populations of *R. evertsi* from these two sites respond similarly to sodium arsenite.

DDT, which is known to be not particularly effective against this tick at 0.2 per cent., appeared to exert no controlling effect on adults from Riverdale and Tayside although there was a slight reduction of the immature stages at both sites. From these results it was concluded that populations of the tick from Riverdale and Tayside responded similarly to DDT.

At the Riverdale site, toxaphene (0.25%) and γ BHC (0.03%) considerably reduced larval, nymphal and adult infestations after three consecutive weekly applications, whereas no such change took place in any stage of *R. evertsi* on the control group of cattle. At the Tayside site, toxaphene and γ BHC at the

same concentrations had practically no effect on larval, nymph or adult counts, which remained as high as those on the untreated control cattle.

Dieldrin at 0.10 per cent. considerably reduced larval infestation, eliminated nymphs and reduced the adult infestation after one treatment at Riverdale but appeared to have had little effect on the tick at Tayside.

TABLE II.

Assessment of larval and nymphal populations and counts of adults of *R. evertsi* on groups of cattle from the farms Tayside and Riverdale, hand dressed with several insecticides.

Insecticide	Date of application	Tayside (average from three head of cattle/group)			Date of application	Riverdale (average from two head of cattle/group)		
		Larvae	Nymphs	Adults		Larvae	Nymphs	Adults
Control (untreated)	21.viii.59	+++	+++	29.6	15.ix.59	+++	+++	33.5
	28.viii.59	+++	+++	29	22.ix.59	+++	+++	44.5
	4.ix.59	+++	+++	24.3	29.ix.59	+++	+++	50.5
	11.ix.59	+++	+++	32.3	6.x.59	+++	+++	40
	18.ix.59	+++	+++	22				
γ BHC (0.03%)	21.viii.59	+++	+++	25.6	15.ix.59	+++	+++	61.5
	28.viii.59	+++	+++	31.6	22.ix.59	+	0	37
	4.ix.59	+++	+++	20.3	29.ix.59	+	0	34.5
	11.ix.59	+++	+	20	6.x.59	+	0	22
	18.ix.59	+++	+++	23				
Toxaphene (0.25%)	21.viii.59	+++	+++	31	15.ix.59	+++	+++	50.5
	28.viii.59	+++	+	27	22.ix.59	++	+	21.5
	4.ix.59	+++	+++	25.3	29.ix.59	+	+	25
	11.ix.59	+++	+++	33.3	6.x.59	+	+	25.5
	18.ix.59	+++	+++	28.3				
p,p' DDT (0.20%)	21.viii.59	+++	+++	15	15.ix.59	+++	+++	22
	28.viii.59	+++	+	16.6	22.ix.59	+++	+++	43
	4.ix.59	+++	+	13.6	29.ix.59	+++	+++	32
	11.ix.59	+++	+	13	6.x.59	+	++	25.5
	18.ix.59	+++	++	19				
Sodium arsenite (0.16% As ₂ O ₃)	21.viii.59	+++	+++	20	15.ix.59	+++	+++	49.5
	28.viii.59	+++	++	15.6	22.ix.59	++	+	19
	4.ix.59	+	+	6.6	29.ix.59	++	++	16
	11.ix.59	++	0	14.3	6.x.59	++	+	18.5
	18.ix.59	+	0	12.6				
Dieldrin (0.10%)	21.viii.59	+++	+++	28.6	15.ix.59	+++	+++	36
	28.viii.59	+++	+++	25	22.ix.59	+	0	25

+ = 0—25 approx.
 ++ = 25—60 "
 +++ = 60—600 "

Laboratory experiments.

Adults of *R. evertsi*.

Using an immersion technique developed for use with adults of the blue tick, *Boophilus decoloratus*, (Whitnall & Bradford, 1947), the response to a number of insecticides of fully engorged adult females of *R. evertsi* collected from the farms Tayside and Riverdale was compared. Results of these tests are presented in

26 21

Table III. The most valid criterion of effectiveness of the various insecticides is the percentage of the treated ticks which failed to produce viable eggs, and this has been called the percentage control.

These results indicated that adult females of *R. evertsi* from Tayside, when compared with those from Riverdale, were considerably more tolerant of toxaphene at all three concentrations tested, and of γ BHC and dieldrin at the concentrations used. However, sodium arsenite and Delnav (2,3-p-dioxane S,S-bis(O,O-diethyl phosphorodithioate)) were equally effective on both populations.

TABLE III.

The effect of a number of insecticides on the fully engorged adult females of *R. evertsi*, obtained with a laboratory immersion technique.

Treatment	Tayside				Riverdale			
	No. of ticks	No. of ticks laying	No. of egg batches hatched	Per-centage control	No. of ticks	No. of ticks laying	No. of egg batches hatched	Per-centage control
Toxaphene 0.25%	20	19	15	25	35	7	3	91.4
Toxaphene 0.5%	10	8	7	30	10	0	0	100
Toxaphene 1.0%	10	8	4	60	10	1	1	90
γ BHC 0.03%	20	20	20	0	35	8	7	80
As ₂ O ₃ 0.16%	10	0	0	100	5	1	0	100
Delnav 0.05%	10	5	2	80	25	7	7	72
Dieldrin 0.1%	10	10	10	0	25	12	11	56
Control (water)	10	10	10	0	20	20	20	0

Larvae of *R. evertsi*.

Larvae were bred under constant conditions (25°C. and 80% R.H.) from fully engorged adults collected in the field. Larvae ranging in age from between 15 and 35 days were subjected to an immersion technique similar to that used for larvae of *B. decoloratus* (Whitehead, 1958). Batches of between 50 and 100 larvae were used for each concentration of insecticide. Tests with each insecticide were replicated between three and five times, depending on the availability of larvae.

As was the case with *B. decoloratus*, satisfactory results with sodium-arsenite solutions could not be obtained using this immersion technique. In investigations of insecticide resistance in *B. decoloratus*, determination of resistance to sodium arsenite was achieved by using adults, large numbers of which were usually available.

In respect of *R. evertsi*, of which large numbers of adults were never available, the development of a test procedure for determining the effect of sodium arsenite on larvae was necessary. The following procedure was found to give reproducible results.

Batches of approximately 50 larvae were placed between two sheets of 7-cm. filter paper (Whatman no. 1). The periphery of the two sheets of filter paper was crimped between a set of meshing cogs, resulting in a saucer-shaped cell in which a batch of tick larvae was confined. The filter-paper cell was placed on a glass plate, concave surface uppermost, and treated from a pipette with 0.5 ml. of the appropriate sodium-arsenite solution. Immediately after treatment the filter-paper cells were covered with the lid of a 7-cm. petri dish. Mortality counts were made after 72 hours' storage at a temperature of 25°C. and 80 per cent. R.H. To facilitate counting it was found most satisfactory to dry out the cells slightly

by removing the petri-dish covers six hours before counting. Control batches, using water in place of the sodium-arsenite solutions, were included in all tests. Mortality in the controls never exceeded 5 per cent.

The results obtained with sodium arsenite are not comparable with tests with other insecticides because of the difference in technique but they do serve as a valid comparison of response of different populations of larvae to sodium arsenite.

The results of tests with larvae of *R. evertsi* in respect of response to some of the insecticides already mentioned, and also to Sevin (1-naphthyl N-methyl-carbamate), are presented in the form of dosage-probit mortality curves (figs. 1 to 6). Larvae were bred from adult females of *R. evertsi* collected from the farm

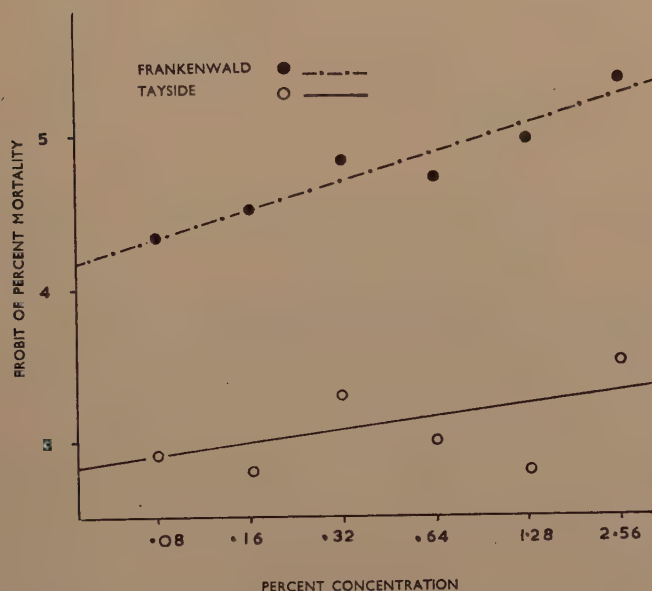


Fig. 1.—The effect of a range of concentrations of toxaphene on larvae of *R. evertsi*.

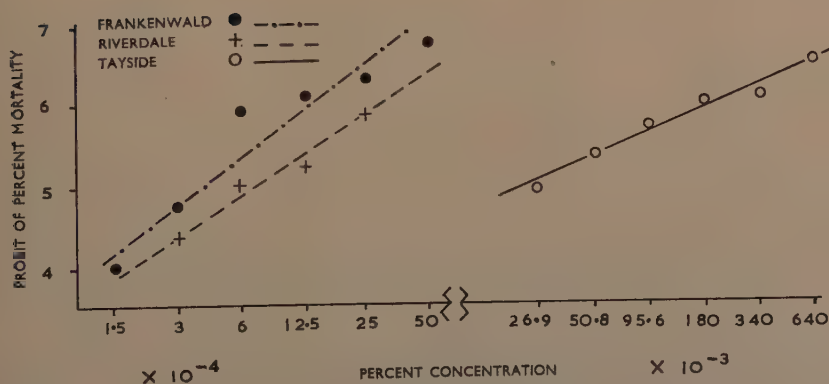


Fig. 2.—The effect of a range of concentrations of γ BHC on larvae of *R. evertsi*.

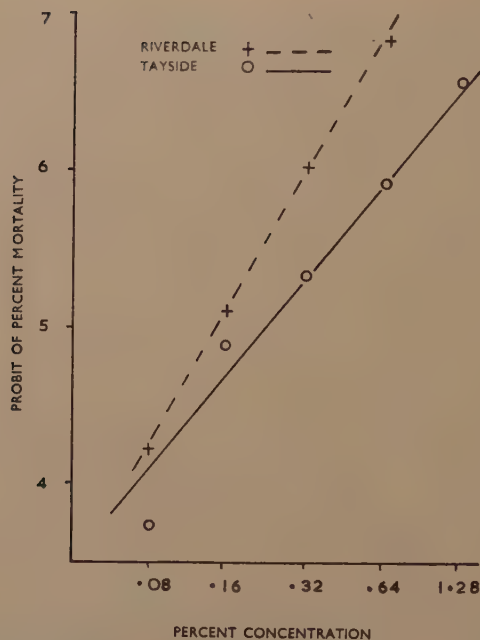


Fig. 3.—The effect of a range of concentrations of sodium arsenite (as % As_2O_3) on larvae of *R. evertsi*.

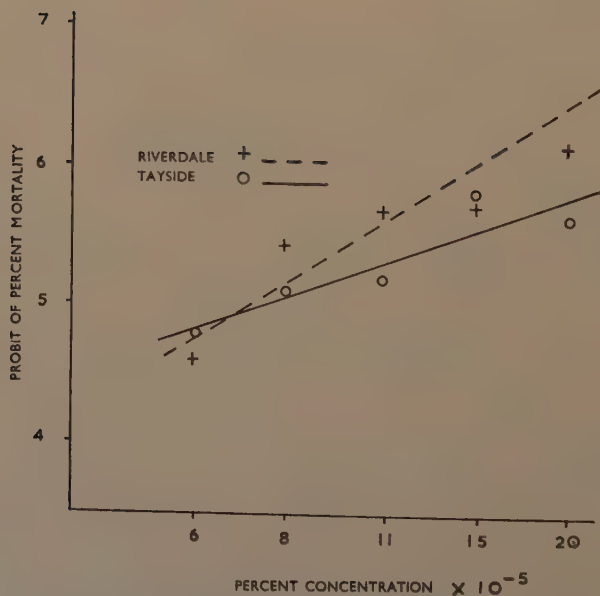


Fig. 4.—The effect of a range of concentrations of Delnav on larvae of *R. evertsi*.

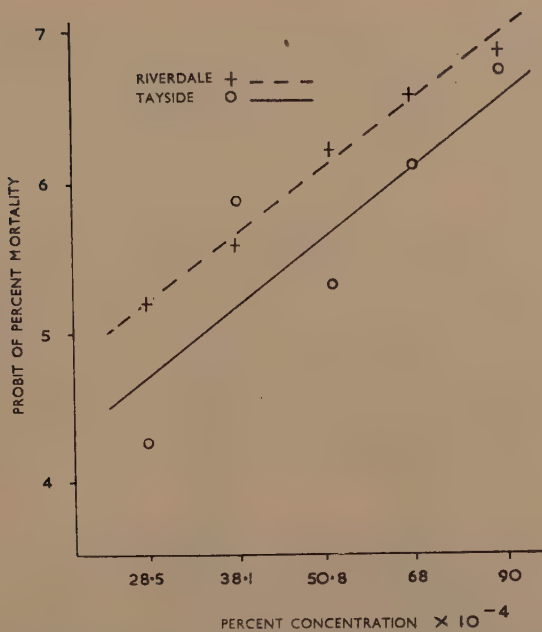


Fig. 5.--The effect of a range of concentrations of Sevin on larvae of *R. evertsi*.

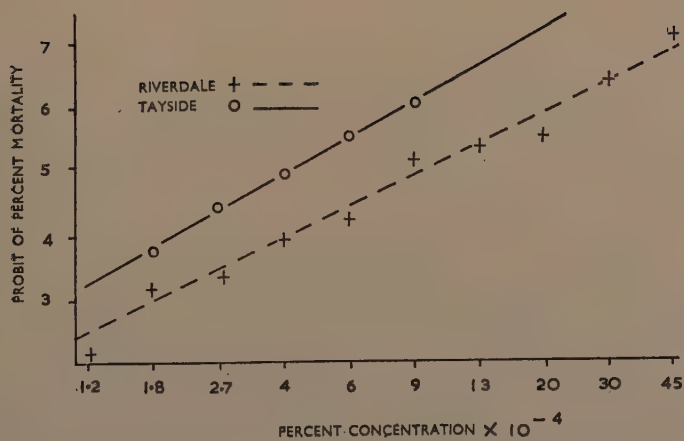


Fig. 6.—The effect of a range of concentrations of p,p'DDT on larvae of *R. evertsi*.

Tayside, where toxaphene resistance had been suspected, and from the farms Riverdale and Frankenwald, where toxaphene treatment apparently maintained satisfactory field control.

The concentration of insecticide required to produce 50 per cent. mortality (LC50), together with a factor of increased tolerance, which is expressed as a ratio of LC50 values when the lowest is equated to 1, are presented in Table IV.

TABLE IV.

The effect of several insecticides on larvae of different populations of *R. evertsi*.

Insecticide	Origin of larvae	LC50 (% concentration)	Factor of increased tolerance
Toxaphene	Frankenwald	0.9536	1
Toxaphene	Tayside	Unattained	7,000,000 by extrapolation
γ BHC	Frankenwald	0.0040	1
γ BHC	Riverdale	0.0073	1.8
γ BHC	Tayside	0.0250	62.5
Sodium arsenite (as As_2O_3)	Riverdale	0.1444	1
Sodium arsenite (as As_2O_3)	Tayside	0.2243	1.55
Delnav	Riverdale	0.00007	1
Delnav	Tayside	0.00007	1
Sevin	Riverdale	0.0026	1
Sevin	Tayside	0.0037	1.42
DDT	Riverdale	0.0009	2.2
DDT	Tayside	0.0004	1

The tests with larvae of *R. evertsi* indicated that the Tayside population was highly resistant to toxaphene and moderately resistant to γ BHC but was about as sensitive to sodium arsenite, Delnav, Sevin and DDT as was the Riverdale population.

Discussion.

Both the field and the laboratory investigations of adult and immature stages of *R. evertsi* have clearly indicated that the population of this red tick from the farm Tayside in the East London district has developed a high degree of tolerance to toxaphene.

The history of chemical control of ticks on Tayside is as follows:

From 1920 to 1945, sodium arsenite was used exclusively. As the result of the development of resistance to arsenic in *B. decoloratus*, BHC was introduced and used over the period 1946 to 1948. With the development of resistance to BHC in this tick, DDT was introduced and used from 1949 to 1955. Toxaphene preparations were first used at Tayside in mid-1955 and were used continually until mid-1959, when the first indication of resistance to toxaphene in *R. evertsi* was observed. It thus appears that four years of continuous treatment with toxaphene has resulted in the selection in this locality of a population of *R. evertsi* that is resistant to toxaphene, and also to γ BHC and dieldrin. Dieldrin had never been used for the field control of ticks on this farm, but γ BHC had been used for two years, six years before the introduction of toxaphene, and this may have contributed to the selection of a population resistant to the chlorinated cyclic hydrocarbon group of insecticides. The Tayside population of *R. evertsi* is, however, not resistant to DDT, sodium arsenite, the organophosphorus compound Delnav and the carbamate Sevin. This pattern of cross-resistance is similar to that found in *B. decoloratus* (Whitehead, 1959).

Conclusion.

Considerable evidence is available from published literature supporting the theory that the development of insecticide-resistant populations is the result of the selection of pre-adaptive characteristics. The rapidity with which a resistant population will develop is dependent on the selection pressure. In South Africa 'one-', 'two-' and 'three-host' species of ticks usually occur together, and control measures are designed to be effective against all types of ticks irrespective of the biological characteristics of individual species. It follows that, as the frequency of treatment is the same for all species, selection will be greatest in respect of the one-host species and least with the three-host species.

Up until 1959, the one-host tick *B. decoloratus* was the only species to have developed insecticide-resistant populations. It was predicted (Purchase, 1955) that "if any 'multi-host' ticks do, in the future, acquire resistance then of these the last to do so will be the Bont-legged (*Hyalomma*)" as only the adult stages are commonly present on stock. This implied, as a corollary, that two-host ticks might be the next to develop tolerance. The results presented in this paper agree with this prediction.

but all stages seen to be on cattle - cf. 1290746-757

Summary.

Early in 1959, observations on the farm Tayside, in the East London district of South Africa, suggested that populations of the 'two-host' red tick, *Rhipicephalus evertsi* Neum., were more difficult to control with toxaphene preparations than they had been in the past. Resistance to toxaphene was suspected, and both field and laboratory experiments were carried out to investigate this possibility. Field trials indicated an increase in tolerance by Tayside populations of the tick to toxaphene, γ BHC and dieldrin, but showed no increased tolerance to sodium arsenite or DDT. Similar results were obtained in laboratory experiments where Tayside adults were compared with those of other populations of the tick known to be sensitive to insecticides. Laboratory experiments with larvae indicated a high degree of resistance to toxaphene and γ BHC in the Tayside population, but no increased tolerance to sodium arsenite, Delnav, Sevin or DDT could be detected. This pattern of cross-resistance is similar to that occurring in resistant populations of *Boophilus decoloratus* (Koch).

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References.

- HANSENS, E. J. (1956). Chlordane-resistant brown dog ticks and their control.—*J. econ. Ent.* **49** pp. 281–283.
- PURCHASE, H. S. (1955). Some thoughts on ticks and their practical control. Part I.—*Bull. epiz. Dis. Afr.* **3** pp. 226–230.
- WHITEHEAD, G. B. (1958). Acaricide resistance in the blue tick, *Boophilus decoloratus* (Koch). Part I.—*Bull. ent. Res.* **49** pp. 661–673.

47 23

WHITEHEAD, G. B. (1959). The development and mechanism of insecticide resistance in the blue tick, *Boophilus decoloratus* Koch.—*J. S. Afr. vet. med. Ass.* **30** pp. 221-234.

WHITNALL, A. B. M. & BRADFORD, B. (1947). An arsenic-resistant tick and its control with gammexane dips.—*Bull. ent. Res.* **38** pp. 353-372.

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36 21

STUDIES ON THE BIONOMICS OF THE JUTE STEM GIRDLER,
NUPSERHA BICOLOR POSTBRUNNEA DUTT* (COL., LAMIIDAE).

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Jute stem girdler, *Nupserha bicolor postbrunnea* Dutt, is a troublesome pest of *olitorius* jute (*Corchorus olitorius*) and is now spread all over the *olitorius* tracts of the different States of the Indian Union since it first became established on the crop. The pest is present throughout the whole jute season, and the ovipositing female causes loss of stem length by girdling the susceptible portion of jute stem (Dutt, 1956a). Beeson & Bhatia (1939) reported *Phaseolus aconitifolius*, *P. aureus*, soy bean and sunn-hemp as food-plants of *N. bicolor* and its distribution as Java and India (Pusa). According to them, *Nupserha* sp. reported by Dutt (1915) on soy bean, and the beetle referred to by Fletcher (1918) on *Vigna unguiculata* belong to the same species. Recently, Breuning (1950a) has reported as many as 14 species of *Nupserha* from the Indian Union, but none of them was from West Bengal nor is any one of them a pest on any agricultural crop. The present subspecies thus appears to be the most important member of the genus, since it has attained the status of an agricultural pest in recent years.

The origin of the infestation in jute.

The pest was not known on jute till 1949, when it was recorded in West Bengal. The question arises as to its origin and how it has become established on jute. A search, in this connection, was made for its alternative hosts in West Bengal, where the pest was first recorded on *olitorius* jute. Most of the food-plants recorded so far, namely *Sesbania aegyptiaca*, *S. bispinosa* (local name—dhaincha), *Aeschynomene aspera*, *Crotalaria juncea* and *C. saltiana*, belong to the Leguminosae. Jute, however, is an exception, since it belongs to the Tiliaceae. Casual incidence was also noted on *Hibiscus cannabinus* (Malvaceae).

At the time when these host-plants were recorded, the highest level of incidence was noted on *S. aegyptiaca*. This plant was, therefore, considered to be the most favoured amongst the food-plants then known. Only casual incidences were recorded in others. Had the pest become established on the agricultural crops like *C. juncea*, *C. saltiana*, *H. cannabinus* or *S. bispinosa* a long time ago, it would have spread to jute much earlier, as these crops are often grown near jute fields and at the same season. It appears probable that the pest was formerly confined to the wild shrub, *S. aegyptiaca*. In response to a campaign, immediately after the partition of India in 1947, to grow more jute, there was a sudden extension of cultivation of jute from 0.652 million acres in 1947 in the Indian Union to 1.163 million acres in 1949 and to 1.951 million acres in 1951. In West Bengal, the acreage of jute rose from 0.266 million acres in 1947 to 0.498 million acres in 1949 and 0.876 million acres in 1951. More than 87 per cent. and 229 per cent. increase in jute acreage in 1949 and 1951, respectively, in West Bengal over the 1947 figure, suggests the probability that the cultivation of jute extended into the neighbourhood of the wild shrub, *S. aegyptiaca*. It therefore seems likely that it was from this shrub that the pest became established

* It is understood from the Commonwealth Institute of Entomology, London, that the authority for the name of this insect is as given here, since it had not been published by Breuning at the time that the early stages were described by Dutt (1956b).

on jute and subsequently on other agricultural crops. *Olitorius* jute has proved to be a very suitable food-plant. A gradual increase of incidence of the pest was later noted on *S. bispinosa*, a green-manure crop of great economic importance.

Relative preference for *Corchorus olitorius* and *Sesbania bispinosa*.

Incidence of the pest in *S. bispinosa* has lately shown a rapid increase. In other alternative food-plants, incidence remains at a much lower level. To assess the relative preference of the pest for the two important agricultural crops, namely *C. olitorius* and *S. bispinosa*, or, in other words, to test the comparative susceptibility of the two food-plants, one field trial was carried out in a paired-plot layout with 12 replications. Plot size was 450 sq. ft. (25 ft. \times 18 ft.). *S. bispinosa* and *C. olitorius* (variety C.G.) were sown broadcast, using a seed rate of 25 lb./acre in the case of the former (larger seed size), and 5 lb./acre in the case of the latter. Weekly observations on the incidence of the pest (girdling and oviposition) were recorded, starting 15 days after germination and continued till maturity, from 16.6 per cent. of the area of each plot, split into suitable units and selected at random after elimination of a 1-ft. border around each plot. Analysis was done on a transformed scale using the formula:

$$y = \sqrt{p+0.5}$$

where,

y = transformed variate,

p = original variate (incidence per cent.).

The first inspection, made on the fifteenth day, showed that no incidence of the pest on either of these crops had taken place up to the end of the second week of growth. From the third to the fifteenth week of growth, incidence remained higher in *S. bispinosa* than the C.G. variety of *olitorius* jute, the difference being significant at 1 per cent. level during the third to the eighth week and during the tenth week of growth. During the ninth and twelfth weeks, incidence difference was significant at 5 per cent. level. During the eleventh week and from the thirteenth week onward, the differences in the two crops were non-significant, though incidence appeared to be higher in *S. bispinosa* (Table I).

TABLE I.

Incidence of *Nupserha b. postbrunnea* in *Sesbania bispinosa*
and *Corchorus olitorius*.

Age of the crop in weeks	Mean on transformed scale		<i>P</i>
	<i>S. bispinosa</i>	<i>C. olitorius</i>	
3	1.4482	0.7554	0.01
4	2.3037	1.0323	0.01
5	1.7953	1.2460	0.01
6	1.8795	1.0907	0.01
7	1.8009	1.1623	0.01
8	1.8242	1.0247	0.01
9	1.3189	0.9391	0.05
10	1.7730	0.9972	0.01
11	1.3490	1.0745	Large
12	1.0429	0.8318	0.05
13	1.4435	1.1526	Large
14	1.1734	0.9196	Large
15	1.1682	0.9981	Large

Stem diameter and oviposition in *Sesbania bispinosa*.

Oviposition in *S. bispinosa* is done in a way similar to that adopted in the case of jute by the egg-laying female girdling the stem at two different levels. While in the case of jute the stem diameter selected for girdling and oviposition ranges from 2 to 4 mm. (Dutt, 1956a), it has been observed that the range in *S. bispinosa* is much wider, and varies from 2 to 7 mm. In the C.G. variety of *olitorius* jute, the portion of the stem falling within the diameter range of 2.6 to 3.0 mm. is most favourable for girdling and oviposition, while, in *S. bispinosa*, the stem diameter most susceptible for girdling and oviposition lies within the range of 3.1 to 5 mm. (fig. 1).

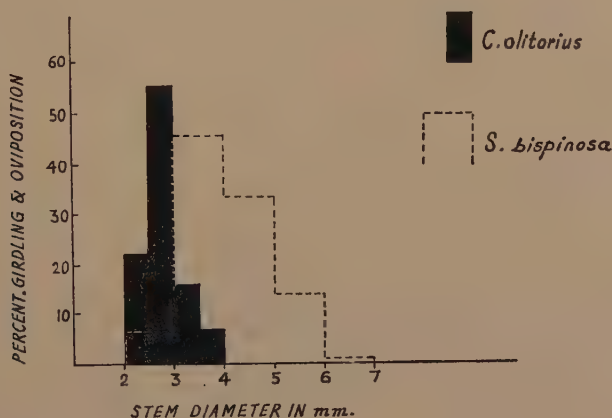


Fig. 1.—Stem diameter and site of girdling and oviposition in *C. olitorius* and *S. bispinosa*.

Relationship between the mandibular length and site of oviposition in *S. bispinosa* and *C. olitorius*.

It has been shown in earlier observations (Dutt, 1956a) that the ratio between the mandibular length and the depth of stem tissue from the epidermis down to the periphery of the pith (extra-medullary tissue) determines the site of girdling and oviposition on the stem of the food-plant even though the range of stem diameter selected for girdling and oviposition in different hosts may vary greatly. In view of the well-marked difference in the stem-diameter ranges at the site of oviposition in *C. olitorius* and *S. bispinosa* already mentioned, a detailed study, similar to one undertaken by the author (1956a) in the case of C.G. jute, was taken up to ascertain if the ratio of the mandibular length to the depth of extra-medullary tissue in the stem of *S. bispinosa* falling within the stem-diameter range susceptible to oviposition (2 to 7 mm.) agrees with that observed in C.G. jute in spite of the wide difference in stem-diameter ranges susceptible to girdling and oviposition in the two hosts. Stem-diameter classes selected for observations on *S. bispinosa* were: 2–3 mm., 3.1–4 mm., 4.1–5 mm., 5.1–6 mm., 6.1–7 mm. The results are shown in Table II. The data for *C. olitorius* are derived from Dutt (1956a, Table IV). It may be seen from fig. 1 that the highest rates of oviposition in *S. bispinosa*, namely 45 and 34 per cent., are recorded in the stem-diameter ranges from 3.1 to 4 mm. and from 4.1 to 5 mm., respectively. The ratios of the mandibular length to the depth of extra-medullary tissue of stem in these diameter ranges is 1:0.81 and 1:0.89, respectively. In *olitorius* jute,

maximum oviposition was observed in stems with a much smaller diameter ranging from 2.6 to 3 mm. (fig. 1), but the ratio of mandibular length to depth of extra-medullary tissue in the epidermal furrow and ridge in this stem-diameter range is 1:0.80 and 1:0.99, respectively. Thus the ratios of the mandibular length to the depth of extra-medullary tissue at sites of maximum oviposition in *C.*

TABLE II.

Mandibular length of female of *N. b. postbrunnea* and its ratio to stem diameter and depth of extra-medullary tissue in *S. bispinosa* in relation to oviposition.

Stem-diam. classes (mm.)	Mean depth of extra-medullary tissue (mm.)	Mean mandibular length of beetle (mm.)	Ratio of mandibular length to :		% distribution of oviposition site
			stem-diam. class	depth of extra-medullary tissue	
2-3	0.446	0.654	1 : 3.05- 1 : 4.58	1 : 0.71	6.86
3.1-4	0.531	—	1 : 4.74- 1 : 6.11	1 : 0.81	45.13
4.1-5	0.585	—	1 : 6.26- 1 : 7.64	1 : 0.89	33.93
5.1-6	0.677	—	1 : 7.79- 1 : 9.17	1 : 1.03	13.36
6.1-7	0.725	—	1 : 9.32- 1 : 10.70	1 : 1.10	0.72

olitorius and *S. bispinosa* almost tally in spite of the wide difference between the ratios of mandibular length and stem diameter at these sites. Over the whole range of stem diameter susceptible in the two plants (2.4 mm. for *C. olitorius* and 2.7 mm. for *S. bispinosa* (see p. 767) the ratios of mandibular length to stem

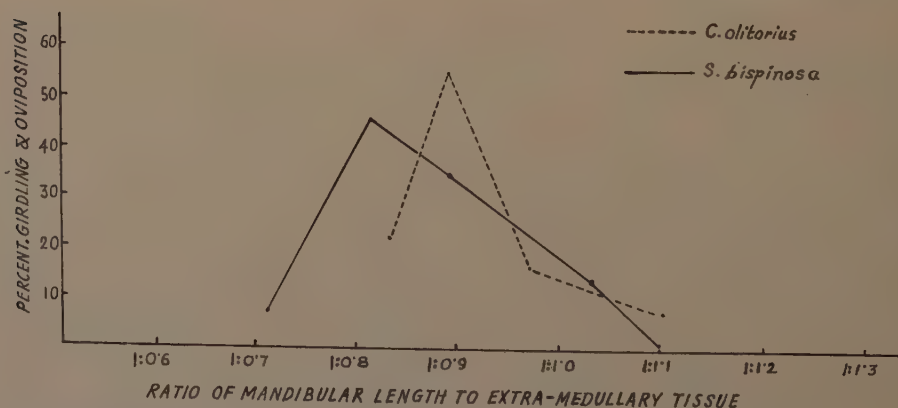


Fig. 2.—Ratio of mandibular length to extra-medullary tissue in *C. olitorius* (mean of ridge and furrow) and *S. bispinosa* follow a similar pattern in relation to incidence. For *C. olitorius*, the ratio for each point is the mean of the two figures given by Dutt (1956a, Table IV), and for *S. bispinosa* it is taken direct from Table II of the present work.

diameter are from 1:3.05 to 1:6.11 for *C. olitorius* and from 1:3.05 to 1:10.70 for *S. bispinosa*, but the ratios of mandibular length to depth of extra-medullary tissue over the same range are from 1:0.75 to 1:1.18 and from 1:0.71 to 1:1.10, respectively. Mean values of the ratios with reference to different stem-diameter classes have been plotted in figs. 2 & 3.

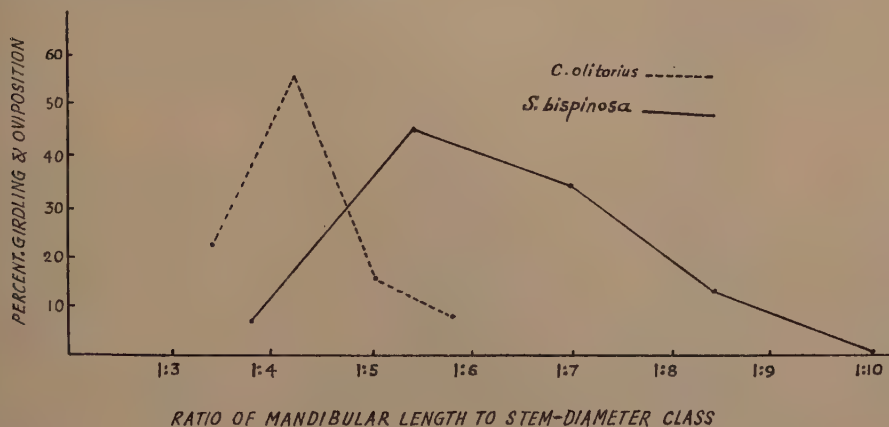


Fig. 3.—Ratio of mandibular length to stem diameter in *C. olitorius* and *S. bispinosa*. For *C. olitorius*, the ratio for each point is the mean of the two figures given by Dutt (1956a, Table IV) and for *S. bispinosa* it is the mean of the two figures in Table II of the present paper.

Acceptability of jute varieties to the adults.

Jute fibres of commerce are obtained from two cultivated species of jute, namely *Corchorus olitorius* and *C. capsularis*. Within each of these species there are well-defined varieties. It has been observed that the adults of the stem girdler attack all the varieties of *olitorius* jute but reject those of *capsularis* (Dutt, 1952). To assess the resistance of varieties of *capsularis* jute to adults, 17 varieties were selected for test. Batches of adults were reared on *olitorius* jute under laboratory conditions and a batch consisting of ten specimens (5 males and 5 females) was released on each *capsularis* variety within a wire-gauze cage. It was found that even under these conditions the adults preferred to die of starvation rather than to accept the *capsularis* jute either as food or for oviposition. In the *olitorius* varieties, used as check, adults thrived and laid eggs (Table III).

Acceptability of varieties of *capsularis* jute to larvae.

To test the acceptability of varieties of *capsularis* jute to the larvae, ten larvae were transferred in an early stage from *olitorius* jute to each of the 17 *capsularis* varieties, under laboratory conditions. These larvae accepted all 17 *capsularis* varieties, and there was no adverse effect on their growth. The larvae subsequently pupated, and adults emerged. Thus the *capsularis* varieties are susceptible to the larvae, but such susceptibility does not alter the unacceptable nature of varieties of *capsularis* jute under field conditions, as the female rejects them for girdling and oviposition (Dutt, 1956b).

Acceptability of varieties of *capsularis* jute to adults raised from larvae reared on *capsularis* jute.

Seventeen batches, each consisting of ten larvae, were successfully reared on *capsularis* jute up to the adult stage. Each batch was reared separately on one

TABLE III.

Acceptability of *capsularis* and *olitorius* jute to adults.

Variety	No. of adults released on each variety	Acceptable (+) or unacceptable (-)
<i>capsularis</i> varieties		
D-154 ..	5♂ + 5♀	—
JRC-212 ..	5♂ + 5♀	—
JRC-13 ..	5♂ + 5♀	—
JRC-320 ..	5♂ + 5♀	—
JRC-321 ..	5♂ + 5♀	—
JRC-322 ..	5♂ + 5♀	—
JRC-412 ..	5♂ + 5♀	—
JRC-48 ..	5♂ + 5♀	—
Assam-16 ..	5♂ + 5♀	—
D-386 ..	5♂ + 5♀	—
Orissa-6J ..	5♂ + 5♀	—
Hewti ..	5♂ + 5♀	—
Jap Red ..	5♂ + 5♀	—
Halmehera ..	5♂ + 5♀	—
Kamardani ..	5♂ + 5♀	—
Fanduk ..	5♂ + 5♀	—
Maniksari ..	5♂ + 5♀	—
<i>olitorius</i> varieties		
C.G. ..	5♂ + 5♀	+
JRO-620 ..	5♂ + 5♀	+
JRO-632 ..	5♂ + 5♀	+
JRO-753 ..	5♂ + 5♀	+
R-26 ..	5♂ + 5♀	+

TABLE IV.

Acceptability of *capsularis* varieties to adults obtained from larvae reared on *capsularis* jute.

Variety of <i>capsularis</i>	No. of larvae reared per variety	No. of adults obtained	Acceptable (+) or unacceptable (-) to :	
			larva	adult
D-154	10	10♂♀	+	—
JRC-212	10	10♂♀	+	—
JRC-13	10	10♂♀	+	—
JRC-320	10	10♂♀	+	—
JRC-321	10	10♂♀	+	—
JRC-322	10	10♂♀	+	—
JRC-412	10	10♂♀	+	—
JRC-48	10	10♂♀	+	—
Assam 16	10	10♂♀	+	—
D-386	10	10♂♀	+	—
Orissa 6J	10	10♂♀	+	—
Hewti	10	10♂♀	+	—
Jap Red	10	10♂♀	+	—
Halmehera	10	10♂♀	+	—
Kamardani	10	10♂♀	+	—
Fanduk	10	10♂♀	+	—
Maniksari	10	10♂♀	+	—

of these 17 varieties after their initial transfer from *olitorius* jute in an early stage. Each batch of ten adults was released in a cage containing the *capsularis* variety on which they had been reared. Although they had passed a major portion of their larval life in *capsularis* varieties, none of the adults in any of these 17 batches accepted the *capsularis* jute, either as food or for girdling or oviposition (Dutt, 1956b) even in the absence of choice (Table IV). They all died of starvation. This observation does not agree with the host-selection principle as enunciated by Craighead (1921, 1923). According to him, adults of several species of CERAMBYCIDAE show a preference for the host on which they have fed as larvae.

Effect of mixed sowing of *capsularis* and *olitorius* jute on incidence.

A *capsularis* variety (D154) and an *olitorius* variety (C.G.) were sown together as a mixed crop in different proportions, to find out if the presence of the unacceptable *capsularis* type can prevent incidence in the acceptable *olitorius* type. There were eight observation plots, each with an area of 180 sq. ft. (18 ft. x 10 ft.). As the seed sizes vary in the two species, mixing in different proportions was done by actual counting of seeds of the two types. Not a single case of incidence was observed on any of the *capsularis* plants grown as a mixed crop with *olitorius* jute, incidence of girdling and oviposition being restricted to the *olitorius* variety. In the plot where only 2 per cent. of the *olitorius* variety and 98 per cent. of *capsularis* jute was sown, i.e., where the *capsularis* jute was highly dominant, incidence could not be prevented in *olitorius* plants, which showed that the pest could select the *olitorius* type from the surrounding unacceptable *capsularis*. Higher percentage incidence was noted in plots with higher proportions of *olitorius* jute, as shown in Table V.

TABLE V.

Incidence of the pest on the varieties of the mixed crop.

Treatment	Proportion (%) of seed in mixture		Percentage incidence	
	<i>olitorius</i> (C.G.)	<i>capsularis</i> (D154)	<i>olitorius</i> (C.G.)	<i>capsularis</i> (D154)
I	0	100	—	Nil
II	2	98	1.00	Nil
III	5	95	4.49	Nil
IV	10	90	5.83	Nil
V	20	80	6.97	Nil
VI	40	60	11.27	Nil
VII	80	20	15.73	Nil
VIII	100	0	15.68	Nil

Incidence in different cultivated types of jute.

To determine the extent of any difference in incidence in jute varieties, a trial was carried out with five *olitorius* types, viz., C.G., JRO-632, JRO-753, JRO-620 and R-26, and five *capsularis* varieties, viz., D-154, Fanduk, Jap Red, JRC-212 and JRC-321, in the same layout. The crop was not harvested at the usual time but was allowed to grow to maturity. Monthly records on the incidence

of the pest were maintained. As was expected, none of the *capsularis* varieties was attacked, but the *olitorius* varieties showed various levels of incidence. Amongst the *olitorius* types, C.G. showed the highest level of incidence, and this was maintained almost throughout the entire season (fig. 4).

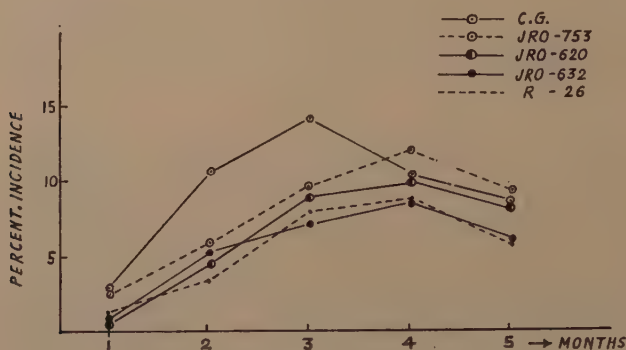


Fig. 4.—Susceptibility amongst the varieties of *C. olitorius*.

Girdling and oviposition in different height groups of *olitorius* jute.

It is found that plants of different heights are not equally chosen by the female for girdling and oviposition. It has been observed that the frequency of girdling is higher in plants falling within the height of 100 cm. to 200 cm. though all classes of plants, young or old, are attacked (Table VI). It is possible that the females prefer a height between 100 cm. to 200 cm. in their spatial distribution, so that the plants that have a suitable depth of extra-medullary tissue within this normal habitat in space are subject to more injury than others.

TABLE VI.

Girdling and oviposition in different height classes of *olitorius* plants.

Height classes (cm.)	Av. height of the class (cm.)	Frequency of girdling		Stem length from the lower girdle to tip (cm.)
		No.	%	
< 51	41.67	15	1.22	12.51
51-100	82.34	114	9.29	16.58
101-150	127.97	525	42.82	16.13
151-200	171.34	440	35.88	16.60
201-250	219.81	122	9.95	17.11
251-300	259.63	10	0.81	14.43

Effect of girdling on the host.

After the girdles have been cut around the stem, the portion of the plant above the lower girdle begins to wither away within three hours and droops down and dies ultimately in about 72 hours. This dead portion may break off or may hang down from the upper end of the unaffected portion of the stem. Unidirectional vertical growth is suspended, and side branches are given out from

the upper end of the unaffected portion of the stem. The number of side branches that appear as a result of girdling increases with the age of the plant and ranges from two to seven. All the branches appear within 30 days of girdling. These side branches, being very thin, are of little value from the point of view of fibre production. Not only is very little fibre obtained from them, but they also make extraction of fibres more difficult.

To assess the rate of growth in height of such affected plants in comparison with normal ones, fortnightly observations were made on 10 healthy and 10 affected plants of the same *olitorius* variety (C.G.) sown on the same date, each plant being 125 cm. tall and 50 days old on the date of damage. Increase in height due to the growth of side branches on injured plants was compared with that of the main stem of the healthy uninjured plants. Fifteen days after damage, when the plants were 65 days old, the injured ones had an average of 1.9 branches, and the increase in height was 12.5 per cent. as against 22.64 per cent. in the uninjured plants without any side branches. Sixty days after damage, when the plants were 110 days old, increase in height was 101.24 per cent. in normal plants, while it was 72.10 per cent. in damaged ones. This increase in height due to growth of side branches is of little value (see above).

As the borer travels down below the lower girdle after eclosion, to feed upon the disintegrating pith tissues, and because the damaged plants can throw out side branches after loss of the apical meristem, it is evident that the presence of borer inside the stem does not cause any apparent harm to the normal functions of the damaged plant.

Soil moisture and its effect on the diapause larva.

Larval diapause, which affects the final autumn generation, and the influence of a high percentage relative humidity in its termination has been reported earlier (Dutt, 1954, 1956b). With the maturation of the jute crop at the advent of winter, the larva, on the eve of diapause, encases itself within a small piece of stem, both ends of which are cut and plugged. This cutting of the stem results in the dropping of the encased larva on to the soil surface of the field.

One laboratory experiment was set up to find out the effect of continued exposure of the diapause larvae to different percentages of soil moisture. For the purpose, diapause larvae encased in jute stem were put under soil of different known percentage moisture contents in glass jars. Each jar was covered with waxed paper and then sealed with paraffin wax to prevent loss of moisture. As an additional safeguard, the sealed jars were kept in different chambers wherein different percentages of relative humidity were maintained. It may be seen from Table VII that, in soil with moisture content up to 3 per cent., termination of the larval diapause did not take place. In soils with moisture contents between about 5 and 18 per cent., diapause development proceeded, and pupation and emergence of adults started after about three or four months. It appears that, if favourable soil-moisture content brings about the termination of diapause, under the conditions of the experiment a prolonged period of diapause development must first intervene.

Adults emerged between March and July 1958, and between May and July 1959, from larvae entering diapause in 1957 and 1958, respectively. Observations in the two seasons were concluded on 23rd July in 1958 and on 2nd August in 1959, respectively.

Under continued exposure to moisture, death of diapause larvae is common. This is due to adverse factors such as decomposition of the jute-stem casing and fungal growth. Some of the larvae exposed to soil-moisture contents of 13 per cent. and upwards were found dead, during the later exposure period, with the body

extended and flaccid. This condition is referred to in the text and in Table VII as hydration. Under continued exposure to soil with the highest moisture content tested (20%), hydration of all the dormant larvae occurred, and this appeared to be the primary cause of their death. At the dates when observations were concluded, some of the larvae in soil of low moisture content were still alive. When such larvae are exposed to soil of higher moisture content, diapause development and morphogenesis proceed.

TABLE VII.

Effect of continued exposure of diapause larvae to soil moisture (mean of two replications).

Soil moisture (%)	Av. no. larvae exposed	Time of onset of diapause	Date of exposure to moisture	R.H. (%) maintained in chambers for keeping sealed jars	No. adults emerged	Remarks
1.25	6	Nov. 1958	2.ii.59	60	0	Dead or in diapause stage
1.46	9	Nov. 1957	24.xii.57	60	0	do.
2.40	6	Nov. 1958	2.ii.59	60	0	do.
3.08	9	Nov. 1957	24.xii.57	60	0	do.
5.02	9	Nov. 1957	24.xii.57	70	1	
5.19	6	Nov. 1958	2.ii.59	70	3	
7.08	9	Nov. 1957	24.xii.57	70	1	
8.74	9	Nov. 1957	24.xii.57	80	3	
10.25	9	Nov. 1957	24.xii.57	80	4	
11.02	6	Nov. 1958	2.ii.59	95	6	
11.53	9	Nov. 1957	24.xii.57	95	2	Fungal attack
12.98	9	Nov. 1957	24.xii.57	95	0	Fungal attack & hydration
14.24	9	Nov. 1957	24.xii.57	100	1	do.
17.12	9	Nov. 1957	24.xii.57	100	2	do.
18.80	9	Nov. 1957	24.xii.57	100	3	do.
20.00	6	Nov. 1958	2.ii.59	100	0	Hydration

Effect of placement of diapause larvae in different depths of soil under natural conditions.

Ploughing of the jute field after harvest, for sowing of the second crop, often buries the diapause larvae, encased in jute stem, at different depths in the soil. To ascertain if the depth at which a larva is buried has any effect on the larval diapause and subsequent stages, observations were recorded from larvae kept under field conditions, at depths of 0, 2, 4 and 6 in., which are within the depth range turned over during ploughing. A small piece of land selected for the experiment was thoroughly dug over. Twelve earthen flowerpots, 12-in. diameter at the top and 11 in. high, from which the bottoms had been completely removed, were buried in the soil up to the rim. Larvae were placed at the required depth in soil within the pots. The purpose of the pots was the protection of the larvae against predators in the soil. The lower end of a cloth cylinder was tied over the rim of each pot, the upper end being tied and hung from a suitable horizontal support overhead in order to protect the larvae exposed on the soil surface from removal by any agency and to catch the adults after emergence, which took place in June. It may be seen from Table VIII that the chances of survival of the dormant larvae at the surface of the soil (0 in.) are comparatively less than those placed at lower depths, since they either suffer predation or die,

probably as the result of desiccation. It was observed that, under natural conditions, incidences of fungi or hydration of the dormant larvae were much lower than in larvae exposed continuously to soil with higher moisture content in the laboratory, and that mortality was mostly due to the activities of predators.

TABLE VIII.

Effect of soil depths on the diapause larvae (mean of 3 replications).

(a) Biological data.				
Soil depth (in.)	Av. no. of larvae	Time of onset of diapause	Date of placement under soil	Av. no. adults emerged
0	7	Nov. 1958	3.i.59	Nil
2	7	Nov. 1958	3.i.59	3.0
4	7	Nov. 1958	3.i.59	5.3
6	7	Nov. 1958	3.i.59	4.3

(b) Meteorological data.				
Total rainfall (in.) between placement and emergence	Soil Temp. (°C.) at 2-in. depth during the period of experiment			
	Morning		Evening	
	Max.	Min.	Max.	Min.
Jan. — 1.14	18.2	6.6	28.8	17.6
Feb. — 0.88	20.1	8.3	29.9	25.4
Mar. — 0.19	26.3	11.0	37.1	28.2
Apr. — 1.26	29.2	21.2	41.6	28.9
May — 3.33	30.3	25.3	42.1	28.7
June — 14.63	29.4	25.0	34.8	23.8

Extent of damage by a single female.

Since damage to the crop is caused by girdling, and this only takes place during oviposition, it is apparent that, as only one egg usually is laid per plant, a single female will damage as many plants as she lays eggs. The average number of eggs laid is 35. Egg-laying starts about 8 to 10 days after emergence of adults. An interval of from 4 to 48 hr. always elapses between deposition of one egg and the next. The full quota of eggs is laid in the course of 13 to 23 days. The pattern of egg-laying is shown in fig. 5. Matings are frequent under laboratory conditions although the female has a well developed spermatheca.

Eggs.

Eggs are laid singly inside the stem. The egg is yellowish in colour, elongate, slightly curved and with rounded ends. The anterior half is slightly tapered. The egg measures 1.5 mm. to 1.7 mm. in length and 0.4 mm. to 0.5 mm. across the middle. The incubation period varies from 3 to 4 days at $28.9 \pm 2^\circ\text{C}$. (Table IX).

Girdling and egg-development.

To verify the effect of girdling on the development of the egg, one small laboratory trial was carried out. For the purpose, freshly laid eggs were immediately transferred from *olitorius* plants (C.G.) to the same variety with

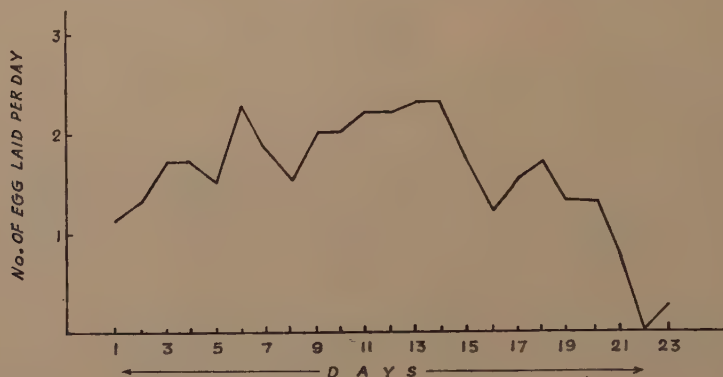


Fig. 5.—Multimodal nature of oviposition pattern (mean of six observations).

similar stem diameter at the rate of one egg per plant. By means of a longitudinal slit, each egg was placed in the periphery of the pith of a fresh plant which was not incised by any girdle. Sterilised scalpels and needles were used during every operation. The effect on egg-development of this transfer to an ungirdled

TABLE IX.

Incubation period of eggs.	
Incubation period (days)	Eclosion (%)
3	36.7
4	63.3

stem was recorded and the result presented in Table X, which shows that only 14.3 per cent. of eggs developed after the transfer.

It was possible that the failure of egg development in these plants might be due to injury to the eggs during the transfer and not to the fact that the plants

TABLE X.

Effect of transfer of eggs to ungirdled *olitorius* plants.

Eggs transferred (no.)	Eggs developed		Eggs failed to develop	
	(no.)	(%)	(no.)	(%)
42	6	14.3	36	85.7

were ungirdled. Another experiment was therefore carried out, in which two sets of *olitorius* plants were used for insertion of eggs. These sets were: (i) plants with two artificial girdles cut down to the vascular bundles so as to stop the flow of sap; (ii) plants with only two artificial scratches around the stem such that they would not stop the supply of sap. In both the cases, insertion of eggs was made through a longitudinal slit in between the two girdles or scratches. The slit portion of the stems that had received scratches only was covered with a non-absorbent cotton pad loosely tied to prevent loss of moisture. Altogether 100 transfers were made, 50 in each set. In the girdled plants, *i.e.*, where the supply of sap was arrested, 82 per cent. of the eggs developed, while in the other set, 22 per cent. developed. The difference in the percentage of the eggs developed in the two sets is appreciable, and this suggests that the girdles are cut to arrest the flow of sap and thus to afford suitable conditions for development of the egg. This is in conformity with other reports (Essig, 1942; Duffy, 1953). Besides, as in this case the larva, after hatching, travels downwards below the level of the lower girdle, it seems that the rings are cut for the welfare of the egg. It has been observed, under the experimental conditions, that in stunted plants without ring-cuts, in which the moisture content is much less than in succulent, quick growing ones, eggs often develop normally and larvae hatch out in the absence of girdles. On the other hand, eggs introduced into succulent plants without any girdles are often crushed by the callus tissues developing in the region of the slit. Under natural conditions, plants with healed indentation wounds at the level of the two girdles are also met with. In such plants, neither does the egg develop nor is there any drooping of the apical portion of the stem above the girdle.

Inter-girdle stem length in *olitorius* jute.

As the girdle appears to be cut to bring about suitable conditions for development of the egg, a large number of attacked stems was measured for the length between the girdles (inter-girdle stem length) in four stem-diameter classes within the range of 2 to 4 mm. to see if there were any relationship between stem diameter and inter-girdle stem length. In 1,097 attacked plants examined, the inter-girdle stem length was found to vary from 5 to 27 mm., irrespective of the diameter of the stem, with the majority between 10 and 12 mm. (fig. 6).

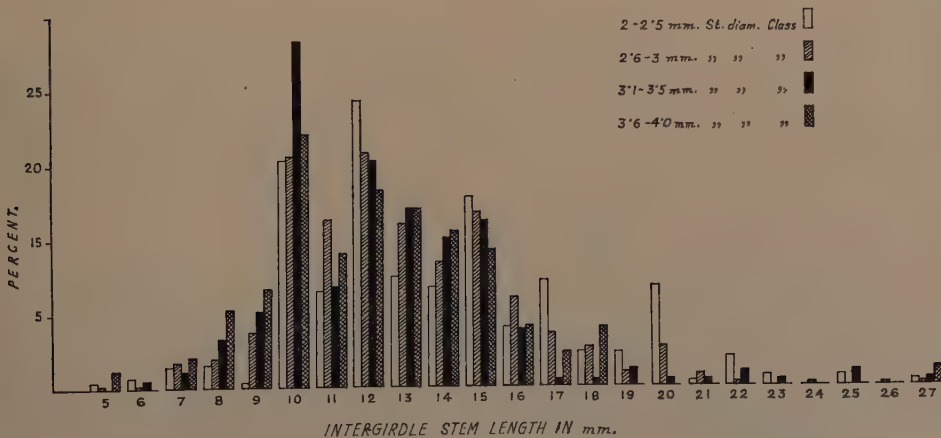


Fig. 6.—Percentage distribution of inter-girdle stem length in each of four stem-diameter classes in *C. olitorius*.

Summary.

Nupserha bicolor postbrunnea Dutt has become established on *olitorius* jute (*Corchorus olitorius*), possibly from its wild food-plant, *Sesbania aegyptiaca*, and from jute it has spread to other agricultural crops. Incidence on the green-manure crop, *Sesbania bispinosa*, has increased so much in recent years that it has surpassed that on *olitorius* jute. The stem diameter most favourable for girdling and oviposition in *S. bispinosa* ranges from 3.1 to 5 mm., whilst in *C. olitorius* it is from 2.6 to 3 mm. In spite of this wide difference in preferred stem diameter, the ratio of mandibular length to depth of extra-medullary tissue of such stems in the two plants agrees well.

All the varieties of *capsularis* jute (*C. capsularis*) are unacceptable to the adults though they are acceptable to the larvae. Adults obtained from larvae reared on varieties of *capsularis* jute also show aversion to *capsularis* types. The pest selects the susceptible *olitorius* from amongst *capsularis* jute when these are grown as a mixed crop. Amongst the *olitorius* varieties, C.G. is the most susceptible. Plants coming within the height range of 100 to 200 cm. are attacked more than others. Girdling causes suspension of unidirectional vertical growth, and this is followed by the appearance of a number of side branches, which are of little value from the point of view of fibre.

Continued exposure of diapause larvae to soil with up to 3 per cent. moisture content inhibited termination of the diapause. In soils with moisture contents between about 5 and 18 per cent., diapause development proceeded, and pupation and emergence of adults started after about three or four months. Under natural conditions, diapause larvae exposed on the soil surface have much less chance of survival than those placed deeper in the soil. It appears that girdling is done to arrest the flow of sap, and thus to afford suitable conditions for the development of the egg.

Acknowledgement.

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References.

- BEESON, C. F. C. & BHATIA, B. M. (1939). On the biology of the Cerambycidae (Coleopt.).—*Indian For. Rec.*, N.S. (Ent.) **5** pp. 1–235.
- BREUNING, S. (1949). Entomological results from the Swedish Expedition 1934 to Burma and British India. Coleoptera: Cerambycidae, Lamiinae, recueillis par René Malaise.—*Ark. Zool.* **42A** no. 15, 21 pp.
- BREUNING, S. (1950a). Descriptions de nouveaux Lamiinaires de l'Inde (Coléoptères).—*Indian For. Rec.*, N.S. (Ent.) **7** pp. 255–265.
- BREUNING, S. (1950b). Nouvelles formes de Lamiinaires (troisième partie).—*Bull. Inst. Sci. nat. Belg.* **26** no. 12, 32 pp.
- CRAIGHEAD, F. C. (1921). Hopkins' host-selection principle as related to certain Cerambycid beetles.—*J. agric. Res.* **22** pp. 189–220.
- CRAIGHEAD, F. C. (1923). The host selection principle as advanced by Walsh.—*Canad. Ent* **55** pp. 76–79.
- DUFFY, E. A. J. (1953). A monograph of the immature stages of British and imported timber beetles (Cerambycidae).—350 pp. London, Brit. Mus. (Nat. Hist.).
- DUTT, H. L. (1915). The soy bean stem-borer.—*Agric. J. Bihar-Oris.* **3** pp. 52–56.

- 138 DUTT, N. (1952). *Nupserha bicolor* Thoms. subsp. *postbrunnea* Breun.: a new pest on jute (*Corchorus olitorius* Linn.).—*Nature, Lond.* **170** pp. 287–288.
- 132 DUTT, N. (1954). Diapause in *Nupserha bicolor* Thoms. ssp. *postbrunnea* Breun. and its bearing on infestation and control.—*Jute Bull.* **17** pp. 286–287.
- DUTT, N. (1956a). Mandibular length in *Nupserha bicolor* Thoms. ssp. *postbrunnea* Breun. (Col., Lamiidae) as the factor in determining the site of oviposition in *Corchorus olitorius*.—*Bull. ent. Res.* **47** pp. 777–783.
- DUTT, N. (1956b). Studies on *Nupserha bicolor* Thoms. ssp. *postbrunnea* Breun. (Col., Lamiidae). IV. Preliminary observations on immature stages and elimination of larval diapause.—*Jute Bull.* **18** pp. 254–256.
- ESSIG, E. O. (1942). College entomology.—900 pp. New York, Macmillan.
- FLETCHER, T. B. (1918). Report of the Imperial Entomologist.—*Sci. Rep. agric. Res. Inst. Pusa 1917–18* pp. 84–116.

THE VARIABILITY OF FLY-ROUND CATCHES IN FIELD STUDIES OF *GLOSSINA*.

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The fly-round has been much used in field studies of tsetse flies, and in a recent paper Ford & others (1959) have described a modification of it, the 'transect fly-round'. This follows arbitrary straight lines and is divided into numerous short sections of equal length. The catching party halts at the posts defining the sections, and catching takes place only at these halts. Old-fashioned fly-rounds (*i.e.*, before Ford & others, 1959) were divided into a few long sections according to the investigator's assessment of the vegetation; a number of stops, to catch flies, were made within each section, but the number and position of these stops were left to the discretion of the catching party. The advantages of the new technique are that it provides a much more detailed picture of the local distribution of tsetse flies than does the older method, that the data appear in a form more amenable to statistical analysis, and that, since catching is more standardised, with less left to the judgment of the catching party, results obtained by different parties should be more closely comparable. 47151

However, it is often the case that an investigator is less interested in a detailed picture of local distribution than in an index of the tsetse population. The fly-round is commonly used for this purpose because it provides the best index we know, but it is subject to wide variation, as is shown by Table IV of Ford & others (1959), which gives the results of doing a fly-round every weekday for a month. The highest catch was found to be more than four times the lowest. It seemed desirable to explore this phenomenon a little further and to attempt some assessment of the magnitude of the errors to which fly-round data are subject.

The experiment described here refers to *Glossina swynnertoni* Aust. and was carried out in the area of preserved thorn-bush known as Block 9 at Shinyanga, Tanganyika. The vegetation of Block 9 has been described by Welch (1959). His detailed numerical data came from No. 5 fly-round, part of which, as described below, was used in the present experiment. Welch states, however, that in general the bush in Block 9 is remarkably uniform, and we have no reason to doubt that the three fly-rounds used in the present investigation are closely comparable. These three fly-rounds (fig. 1) were done every day except Sundays for four weeks. Each round was worked by a separate party, consisting of three catchers, who were unchanged, as far as possible, throughout the experiment. The work was regularly rotated, so that the party that did No. 1 round one day did No. 2 on the second day and No. 5 on the third, returning to No. 1 on the fourth, and so on.

Fly-rounds No. 1, 7,700 yd., and No. 2, 7,500 yd., were divided respectively into 7 and 6 sections of unequal length according to the vegetation. On these two rounds, the catchers stopped to catch at their discretion and the rounds are accordingly designated 'old-fashioned'. The number of stops was not recorded, and may have varied from day to day.

The third fly-round, No. 5, was a transect fly-round, 6,000 yd. long, which was divided into 60 sections each of 100 yds.; it is the second half of the No. 5 fly-round, 12,000 yd., discussed by Ford & others (1959). The catchers on this round stopped only at the end of each section and catching took place only at these stops.

In both methods of carrying out a fly-round, when a stop was made the rear member of the party would immediately turn about to catch the following flies which are commonly visible for a few seconds on the ground close behind the party. If no flies were seen by anybody, the party would at once proceed. If flies were seen, catching would go on until none was left. All flies seen were caught, wherever they might be, on the party, on the ground or on vegetation.

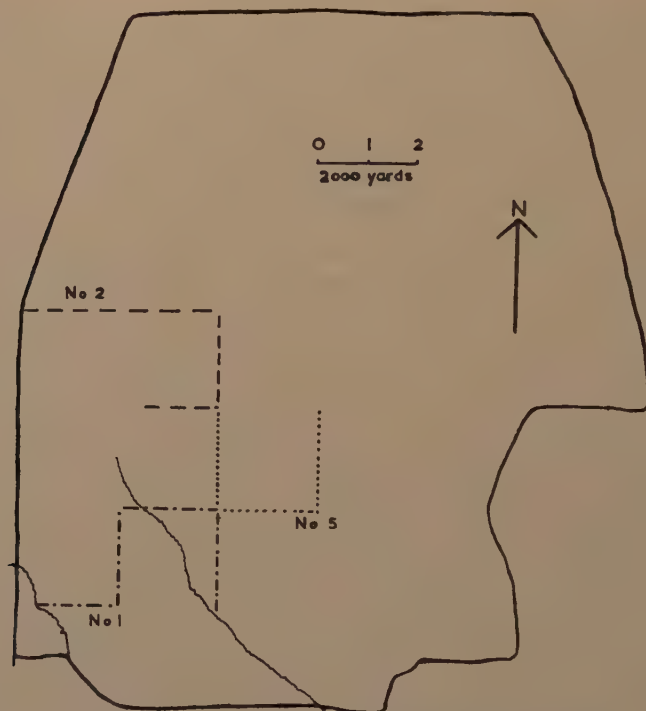


Fig. 1.—Outline map of Block 9 at Shinyanga, showing the three fly-rounds discussed in the text.

Thus the time taken to cover a fly-round was not constant, and though work began at the same time every morning there was some variation in the time at which it ended. Each round took between $3\frac{1}{2}$ and $4\frac{1}{2}$ hours. All flies caught were killed and brought to the laboratory where they were counted and the numbers of each checked against the totals appearing on the field forms. In accordance with our usual practice, the direction in which each round was done was reversed on successive days, so as to minimise the interaction between time and place; for example, if catches decline steadily from the beginning of the round, the reversal shows whether this is an effect of time of day, or of place. Though such effects were not a primary concern of this investigation, the reversal was regularly performed because it was desired to imitate as closely as possible the conditions commonly obtaining in the working use of fly-rounds. For the same reason I did not visit the catchers while they were actually doing the fly-rounds. I was, however, in daily contact with the catchers, and as at the time of the experiment reduction of staff had been going on for some time, the eleven men involved in the experiment were believed to be very reliable. It is

therefore not likely that the variability of the results to be discussed below could have been reduced by either better supervision or by using better staff.

The catches of non-teneral males (*i.e.*, of males judged by feel and appearance to have had at least one meal) on these three rounds are presented in Table I. During the short period of four weeks the true population which is the real object of interest is unlikely to change much, a proposition supported by the

TABLE I.
Catches of non-teneral males of *G. swynnertoni* on three fly-rounds.

	No. 1 (7,700 yards, old-fashioned)	No. 2 (7,500 yards, old-fashioned)	No. 5 (6,000 yards, transect)	Totals	Weekly geometric means
27.iv.59 ..	65	141	286	492	—
28.iv.59 ..	127	65	199	391	—
29.iv.59 ..	88	65	181	334	—
30.iv.59 ..	95	105	229	429	—
1.v.59 ..	45	99	171	315	—
2.v.59 ..	136	176	168	480	400
4.v.59 ..	94	140	449	683	—
5.v.59 ..	152	121	258	531	—
6.v.59 ..	164	204	194	562	—
7.v.59 ..	73	146	304	523	—
8.v.59 ..	176	124	336	636	—
9.v.59 ..	106	148	203	457	541
11.v.59 ..	131	128	410	669	—
12.v.59 ..	117	169	227	513	—
13.v.59 ..	97	159	172	428	—
14.v.59 ..	73	119	312	504	—
15.v.59 ..	148	165	211	524	—
16.v.59 ..	58	161	201	420	503
18.v.59 ..	114	160	446	720	—
19.v.59 ..	155	129	265	549	—
20.v.59 ..	87	186	182	455	—
21.v.59 ..	130	176	394	700	—
22.v.59 ..	118	138	199	455	—
23.v.59 ..	68	105	163	336	521
Geometric mean	119	133	243	—	—
Variance of sample	0.0244	0.0162	0.0199	—	—

The variance given is the variance of the logarithms (to base 10) of the observations.

figures of Table I, which show no obvious trend. The weekly geometric means of the total daily catches of non-teneral males for the four weeks of the experiment were 400, 541, 503 and 521. The large day-to-day variation in catches cannot be related to changes in the true population, and the most satisfactory index of the true population will therefore be that showing the smallest variance.

In the case of No. 5 fly-round, the sources of variation can be explored by the technique of analysis of variance. Since there were 60 stops for catching, and we are considering 24 days' work, the complete table contains 1,440 entries. This is too large to include here, but a copy has been deposited in the archives of the British Museum (Natural History). Before beginning the analysis of variance, each entry in the table was increased by 1, and then transformed into its logarithm to the base 10. The variance was then analysed in two stages. Firstly, as the direction in which the round was done was reversed on successive days, the data were considered as being derived from 12 pairs of occasions. For each pair of occasions, for each section, the transformed value for the second

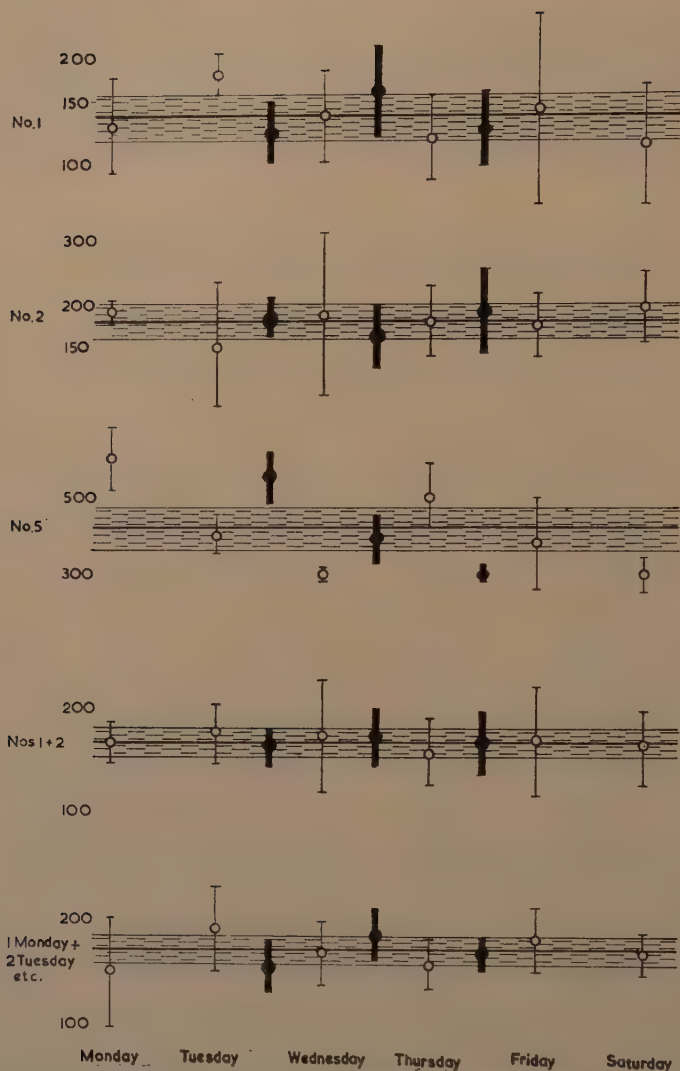


Fig. 2.—The results of the fly-rounds expressed as Apparent Densities (catch of non-teneral males per 10,000 yd.). The numbers are plotted on a logarithmic scale. The horizontal lines represent means for the month, with their fiducial limits (\pm twice standard error) shown as shaded areas, and the vertical lines represent the fiducial limits of the values (shown by circles o or dots •) obtained by working only on certain days.

No. 1: No. 1 fly-round. The thin lines give the results of observing only one day a week, and the thick lines those of working twice a week (Monday and Thursday, Tuesday and Friday, and Wednesday and Saturday).

No. 2: No. 2 fly-round. Symbols as for No. 1.

No. 5: No. 5 fly-round. Symbols as for No. 1.

Nos. 1+2: No. 1 and No. 2 combined and treated as one long fly-round. Symbols as for No. 1.

1 Monday+2 Tuesday: The combined results of doing fly-rounds Nos. 1 and 2 on successive days. The thin lines give the results of doing No. 1 on Monday and No. 2 on Tuesday (drawn in the 'Monday' position), or No. 1 on Tuesday and No. 2 on Wednesday (drawn in the 'Tuesday' position), and so on. The thick line drawn between 'Tuesday' and 'Wednesday' represents the combined results of No. 1 on Monday, No. 2 on Tuesday+No. 1 on Thursday, No. 2 on Friday, and the other thick lines were computed similarly for succeeding combinations of rounds and days. The bottom two rows of the figure represent the same amounts of work, the slight differences being due to differences of arrangement.

day was subtracted from that for the first. For example, the first 7 entries for the first pair of days were:

Sections	61	62	63	64	65	66	67
27.iv.59	1.00	0.60	0.85	0.78	0.90	0.95	0.90
28.iv.59	0.85	0.70	0.95	0.78	0.60	0.70	0.60
Difference	+0.15	-0.10	-0.10	0.00	+0.30	+0.25	+0.30

In this way a new table was made of the differences, containing 720 entries from 12 rows and 60 columns. Positive and negative entries occurred with approximately equal frequency; the grand total was +22.24, so that the mean value was not far from zero. The variance of this table of differences was then analysed as follows:

	Degrees of freedom	Sum of squares	Variance
Between occasions	11	29.9790	2.7254
Between sections	59	8.6467	0.1466
Residual	649	109.7697	0.1691
Total	719	148.3954	

The variance between sections is not significantly different from the residual variance, from which we conclude that reversing the direction of the round had no influence on the catch. We therefore return to the original table, which is analysed as follows:

	Degrees of freedom	Sum of squares	Variance
Between days	23	27.1019	1.1783
Between sections	59	17.2043	0.2916
Residual	1357	109.3727	0.0806
Total	1439	153.6789	

The variances between sections and between days are both very significantly different from the residual variance ($P < 0.001$). The first result means that, as one would expect, some parts of the round were more productive than others. The second result means that the differences between days are greater than can be accounted for by random errors or by interaction between times and places. A similar result (although less certainly established) was interpreted by Ford & others (1959) as showing a difference in 'availability' from day to day, and since we have no reason to believe that large changes in population occurred during the present experiment, it can only be said that the present data, too, indicate short-term changes in availability. Further discussion of availability is deferred to the end of this paper.

The transect fly-round produced a higher catch than the other two fly-rounds, and some of this difference is ascribed to the difference in technique, although previous experience indicated that No. 5 fly-round produced slightly higher catches than No. 2 if they were done in the same way. The raw data (Table I) were converted to their logarithms (base 10) before analysis, as in Williams (1937). The variances of the three sets of observations are not dissimilar, with the value for the transect round (No. 5) lying between those for the other two. The expectation that the more standardised technique of the transect fly-round would produce a lower variance is clearly not realised. It is of interest to note that the data given in Table IV of Ford & others (1959) have a variance in the same range (0.0200). Nevertheless, this experiment has not given an unequivocal comparison between the two methods, since the observed variances could conceivably be properties of the fly-rounds and not of the methods used on those fly-rounds. It

would be possible to devise a Latin-square experiment to eliminate this possibility and also to eliminate possible personal differences between the parties doing the work. This was not done on the present occasion, partly because of the difficulty of applying different methods to the same round on different days (since the presence of posts at 100-yd. intervals must inevitably affect the behaviour of those parties instructed to stop at their discretion) but more because the primary object of the experiment was the more limited one of assessing the errors inherent in fly-round data collected in either way.

A common practice is to work fly-rounds once or twice a week. The results which would have been obtained by doing Fly-rounds 1, 2 and 5 once or twice a week, compared with the results obtained by working six days a week, are shown in fig. 2. One day's work in a week (thin lines) gives but a poor estimate of the mean, often outside the 95 per cent. fiducial limits from 6 days' working (shown as a band in fig. 2). Two days' work a week (thick lines) gives a very marked improvement. Combining the two fly-rounds and treating them as one (e.g., Nos. 1+2 in fig. 2) further reduces the fiducial limits of the mean for the month, and of the means from one day's work per week, while the means from working two days a week (8 days' work in all) are now seen to lie close to the mean from 24 days' work. The results of a procedure very likely to be adopted in practice when staff is limited, namely working one fly-round one day and the other the next, are also shown in fig. 2 (labelled (1 Monday+2 Tuesday, etc.)). Comparison of the bottom two diagrams in fig. 2 might suggest that this practice gives results inferior to those obtained by working both fly-rounds simultaneously, but the total variance of Nos. 1 and 2 combined is slightly but insignificantly greater than that from working them on successive days (0.011 as against 0.010). It therefore appears that no loss of precision results from working two halves of a long fly-round on successive days.

The conclusions drawn from fig. 2 apply to transect as well as to old-fashioned fly-rounds. While the transect fly-round as described by Ford & others (1959) appears to be no better than old-fashioned fly-rounds as an index of the true population, its other advantages are unchallenged and it will therefore always be the preferred method of doing a fly-round. It is concluded that under Shinyanga conditions a fly-round of about 7,500 yd. done daily, or one of 15,000 yd. done twice a week (in two halves on succeeding days if preferred), gives an index of the mean catch which should enable changes of about 2:1 to be detected. On the other hand, a fly-round of 7,500 yd. done once a week could be relied on to detect only grosser changes, of about 5:1. These conclusions cannot, of course, be held to apply necessarily to other species of tsetse, or even to *G. swynnertoni* in other places, but nevertheless the results given by Ford & others (1959) suggest that the same degree of variability is to be expected in fly-round catches of *G. pallidipes* Aust.

In the preceding paragraph, mention was made of recognising changes in the mean catch, not changes in the tsetse population, which is the real object of interest. The relation between fly-round catches and true population is a complex one which is still not fully understood. Ford & others (1959) write of the catch being the product of population density and 'availability'. Estimates of this quantity, 'availability', have in fact been made for at least three species of *Glossina* in various places at particular times (Harley, 1958; Jackson, 1944, 1953; Glasgow, 1954). The values obtained represented mean availabilities over periods of about a month. We have seen above that availability may vary in one place from day to day, and none of these writers was able to estimate the variance of his values for availability. Bearing in mind the magnitude of the variance of the catches recorded above, it follows that estimates of the true population made from catch and availability are subject to wide and undefined errors. The work of Skellam (1958) is an aid to clear thinking. From a plausible mathematical

model, he concludes that an unbiased estimator of the density D is given by $\hat{D} = n/HTV$, when n denotes the number of encounters (or catch, in the special case of tsetse), H is a function of the distance within which an organism is perceptible, T is time and V is the relative velocity of observers and observed. Thus availability is seen to consist of three elements, H , T and V , or more accurately two, H and V , since all estimates of availability have referred to catch per standard length of traverse, which in effect standardises the time. Actually Skellam specifically mentions that his concept, of an area within which the organism studied is perceptible, is probably not applicable to tsetse because they are attracted to the observer. There seems, however, no theoretical difficulty in recognising that H in the case of tsetse is not merely a property of the observer but is a joint property of observer and observed, although the practical difficulties in determining H , and V , are so great that it is unreasonable to expect they will ever be overcome. A further complication in the case of tsetse is that commonly only one sex, the males, are caught in appreciable numbers, and of the males only those in a particular physiological condition, not too hungry and not too replete, are caught (Bursell, E. The behaviour of tsetse flies (*G. swynnertoni*) in relation to problems of sampling*). Thus a constant must be introduced into Skellam's formula, representing the ratio between the total male population and the proportion in a catchable condition. This does not matter at all as long as this proportion remains constant, but if the nutritional status of the population changes with season, as noted by Glasgow & Bursell (1961), then the possibility exists that changes in fly-round catches are in part due to changes in the proportion of males physiologically in a catchable condition. The same considerations apply if a fly-round is being used to follow changes in a tsetse population that is being attacked. Some methods of attack, such as game elimination, certainly alter the nutritional status of the attacked population, and other methods may do so.

Summary.

In an attempt at some assessment of the errors to which fly-round data obtained for the study of populations of *Glossina* are subject, three fly-rounds at Shinyanga, Tanganyika, were worked every weekday for four weeks. The species studied was *G. swynnertoni* Aust. One of the rounds was a 'transect fly-round', the others, the older type, divided into a few long sections according to the vegetation. The catches showed no obvious trend during the experiment, suggesting that the true population had not altered in the period, but in all three rounds there were considerable day-to-day variations in catch and, in this respect, the transect fly-round did not differ from the older method. An analysis of variance of the transect fly-round data showed that the variance between days was greater than could be accounted for by random errors.

By considering separately the data collected on certain days of the week, it is concluded that a 7,500-yd. fly-round done once a week could not detect less than a five-fold change in the mean catch. To detect a two-fold change, a 15,000-yd. fly-round done twice a week would be necessary.

The relation between fly-round catch and true density is discussed. This relation is usually termed 'availability'. Earlier workers have shown that its mean value, over periods of about one month, is not necessarily constant; the present work shows that it varies in one place from day to day.

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References.

- 47 151 FORD, J., GLASGOW, J. P., JOHNS, D. L. & WELCH, J. R. (1959). Transect fly-rounds in field studies of *Glossina*.—*Bull. ent. Res.* **50** pp. 275–285.
- 42 151 GLASGOW, J. P. (1954). *Glossina palpalis fuscipes* Newst. in lake-side and in riverine forest.—*Bull. ent. Res.* **45** pp. 563–574.
- GLASGOW, J. P. & BURSSELL, E. (1961). Seasonal variations in the fat content and size of *Glossina swynnertoni* Austen.—*Bull. ent. Res.* **51** pp. 705–713.
- 46 121 HARLEY, J. M. B. (1958). The availability of *Glossina morsitans* Westw. in Ankole, Uganda.—*Bull. ent. Res.* **49** pp. 225–228.
- 34 196 JACKSON, C. H. N. (1944). The analysis of a tsetse-fly population. II.—*Ann. Eugen.* **12** pp. 176–205.
- 42 149 JACKSON, C. H. N. (1953). A mixed population of *Glossina morsitans* and *G. swynnertoni*.—*J. Anim. Ecol.* **22** pp. 78–86.
- SKELLAM, J. G. (1958). The mathematical foundations underlying the use of line transects in animal ecology.—*Biometrics* **14** pp. 385–400.
- WELCH, J. R. (1959). Observations on the vegetation of Block 9, Shinyanga, Tanganyika.—*Rep. E. Afr. Tryp. Res. Org.* 1958 pp. 64–67.
- WILLIAMS, C. B. (1937). The use of logarithms in the interpretation of certain entomological problems.—*Ann. appl. Biol.* **24** pp. 404–414.

INSECTICIDAL OPERATIONS AGAINST CHIRONOMID MIDGES ALONG THE BLUE NILE.

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and M. QUTUBUDDIN⁴

J. L.

The excessive abundance of the midges sometimes colloquially described as "green nimitti" has been a serious problem in Khartoum and Omdurman, Sudan Republic, ever since the dam was installed on the Blue Nile at Sennar, 150 miles upstream (fig. 1), in 1925. The principal species is *Tanytarsus lewisi* Freeman. The adults appear in immense numbers at the end of November, and remain very abundant until the end of March. Those which emerge from the calm stretch of river at Khartoum are blown by the prevailing north wind into the two-mile frontage between the Grand Hotel and the University, settling in the trees along Sharia el Gasr el Gamhouri (formerly Kitchener Avenue) and back to Sharia Gamaa (formerly Gordon Avenue) (fig. 1, inset). Their swarming at electric lights has made evening activities virtually impossible. Their dried bodies subsequently blown about in Khartoum and Omdurman have caused asthma and more serious allergic reactions.

The larvae of *T. lewisi*, which like the adults are green in colour, develop in the water of the Blue Nile and reach their peak of abundance in February. The pupae are most abundant in December, which could be taken as evidence of two winter generations. Unfortunately, the length of the larval period is still unknown, since the larvae have not survived for more than a few days in captivity. The detailed field studies of Lewis (1957) have shown that the larvae stay on the river bottom during the day and rise towards the surface at sunset; it is thus probable that they travel with the water during the 12 hours of night. Mature larvae rise to the surface where they pupate, usually in the afternoon; the pupae are found near the surface at dusk, and the adults emerge before dawn the following day. Many adults live for about 14 hours, that is, until the following evening, when they die around the lights. Some adults swarm by day, mate, and oviposit on the surface of the river and its backwaters. It is therefore probable that the swarms found along Sharia el Gasr el Gamhouri each evening have emerged early in the morning of that day, after having travelled in the larval stage downriver to Khartoum from a considerable distance. Since the average speed of the Blue Nile during the winter months is approximately 1 m.p.h. along most of its reaches, they could well be expected to have travelled for distances ranging up to 12 miles each night. However, backwaters such as Khor Tuti near Khartoum could produce a constant local supply of midges, Lewis (1957) having found a very high larval population there, particularly of species other than *T. lewisi*, as early as 5th January.

Breeding has evidently ceased when the Blue Nile rises at the end of June. No larvae or pupae could be found in plankton or mud samples in the main channel below and above the Sennar Dam in July 1956. The flood peak is reached in late August, but above-average flow with a high silt content persists until October. It was only in the still water of the Sennar Reservoir itself, at the head

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of the main irrigation canal at Sennar, and in the irrigation canal at Hassa Heissa, that a few *Tanytarsus* larvae could be found in the mud or water in July. The Sennar reservoir is progressively filled during the period from July to the end of November, the dam being partially closed in July and almost completely closed in mid-October. By early November, larvae of *T. lewisi* have become quite abundant in the impounded water, as indicated by samples taken at that time

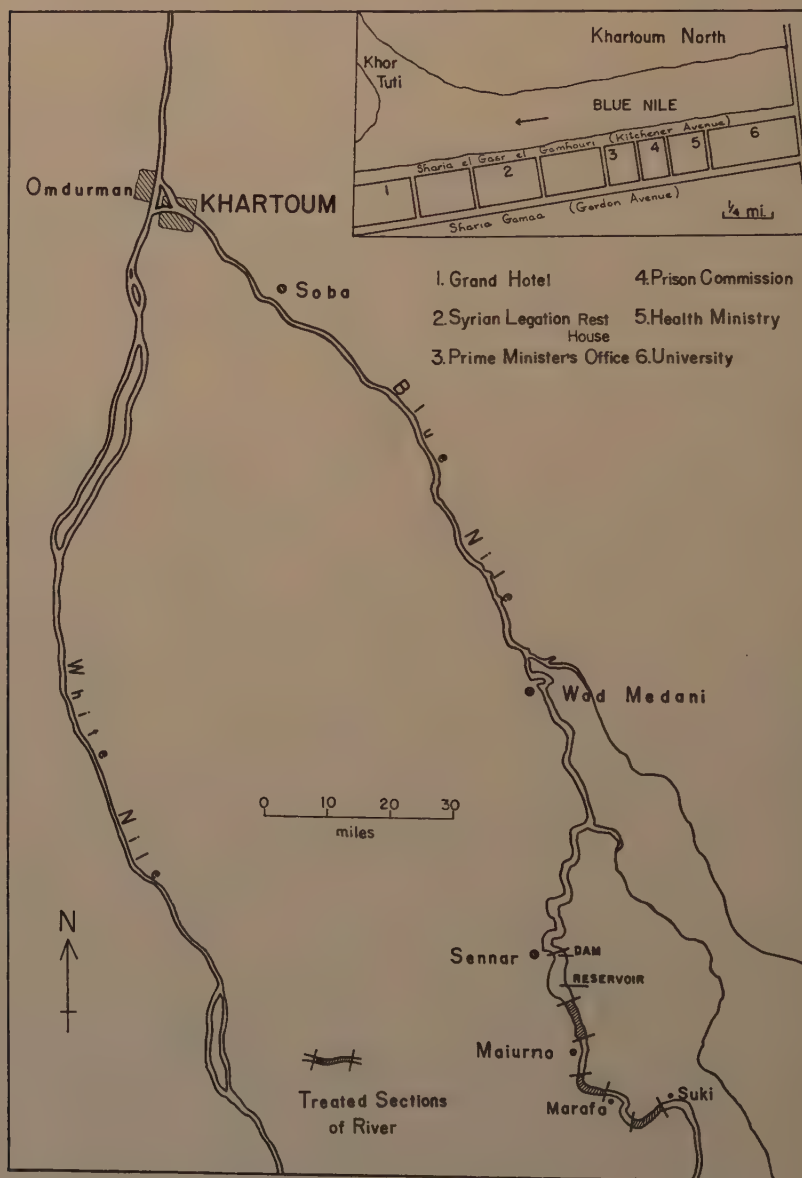


Fig. 1.—Map of the Blue Nile, Sudan, showing sections of river treated above the Sennar Dam. Inset, sketch map of Khartoum.

above Sennar and at Maiurno. Thereafter the impounded water is gradually released to maintain a discharge of between 30 and 12 million cu. m. per day from December to May (Lewis, 1957).

The present paper describes attempts to control *T. lewisi* and associated species with insecticides by various methods. Lewis (1957) found crude, granular BHC to give inconclusive results, and waste lubricating oil to have only slight effect. The methods here described include treatment of the river above Khartoum with DDT, and treatment of the vegetation at Khartoum with DDT applied from the air or from the ground, all of which gave either indecisive or only temporary local control. The main method described was treatment of the Sennar reservoir with DDD, and this was followed by a greatly reduced abundance of midges during the two-year period following the application.

Sampling methods.

Adult populations were sampled at Khartoum every evening from 17th January to 28th February in 1956, from 21st October to 13th March in 1957–1958, and from 21st February to 22nd March in 1959. Light traps were employed, each consisting of an open unpainted wooden box, set on its end, in which was placed an aluminium bowl 8.5 in. in diameter by 4.5 in. deep, with a 100-watt clear electric bulb suspended level with the rim. The lights were switched on from 6 to 8 p.m. daily. The midges caught were dried in the bowl at 100°C. for six minutes and then weighed; 1 g. of this dried material comprised 6,620 adult midges.

The light traps were exposed at five points along Sharia el Gasr el Gamhouri, namely, Grand Hotel, Syrian Legation Rest House, Prime Minister's Office, Prison Commission and Health Ministry (fig. 1, inset). For the 20 days before 11th November 1957, only two stations, on the north and south verandahs of the Health Ministry, were used, but in subsequent concurrent sampling it was found that their average tallied with the average of the five stations. In 1956, sampling was conducted at 10 additional stations in Khartoum and Khartoum North; the averages for the 15 stations are presented as well as those for the five stations. For the 27 days before 18th November 1957, larger dishes were used in the light traps; the catches were therefore corrected to correspond to the smaller dishes, by applying a factor of 0.71 determined experimentally by comparing the catches of each. In 1957, prior to 12th January, the exposure of the traps was only one hour; this was corrected by applying a factor of two, to raise it to correspond with the 2-hour exposure normally employed.

Larval and pupal populations at Sennar, Maiurno and Khartoum were sampled by means of a plankton net 12 in. in diameter towed behind a boat at 2 m.p.h. At Wad Medani, the net was tethered stationary in the main current. Samples were taken between 6 and 8 p.m. and consisted of four tows each of 30 minutes' duration. On a few occasions the sampling period was different, ranging from 24 minutes to 5.5 hours; in these cases the results were corrected to correspond to 2 hours' total sampling time. The results are shown in figs. 3, 4 and 5. Larval populations in the mud were sampled in 1956 by means of a Peterson grab-dredge, 10 in. wide. The larvae recorded were those considered to be *T. lewisi*; the pupae recorded were those considered to be *Tanytarsus*.

River treatment with DDT.

On 20th January 1956, the Blue Nile was treated at Soba, 10 miles upstream of the Khartoum North bridge. A total of 450 lb. DDT was applied in 150 gal. solvent, the spray being made by diluting 3 parts of 40 per cent. DDT concentrate in aromatic oil (sp.g. 1.126) with 1 part of kerosene (sp.g. 0.791), resulting in a mixture of specific gravity 1.040, to which 1.5 gal. Lissapol detergent was added. This was applied from an Auster aircraft flying at 60 m.p.h. and fitted with 25

No. 10 nozzles (the 7 centre nozzles being removed); it was emitted at a rate of 14.7 gal. per min. under a pump pressure of 40 lb. per sq. in., the nozzles being pointed forward. The application was made between 8.20 and 9.45 a.m., when a north wind was blowing across the stream at 10 m.p.h. A total of 42 runs of 13 seconds' duration (*i.e.*, approx. 400 yards length) were made directly across the river, each successive run being located 20 yards further upstream. Since the speed of flow was 1 m.p.h. and the aircraft's turning time was 30 seconds, the distance between the successive swaths laid on the river surface was 20 yards plus 21 yards, *i.e.*, 41 yards, except for the breaks caused by the four reloadings of the aircraft, which occupied in all about 55 minutes. The last swath was located 820 yards upstream of the initial aiming marker on the bank, at which time the first swath should have reached a point 2,500 yards downstream of the first aiming marker.

The length of river water treated was thus 3,320 yards, approximately equivalent to 1 hour 50 minutes of flow at 1 m.p.h. Since the volume flow of the river at Soba was 283 cubic metres per second (data for 12th January, Egyptian Irrigation Department) the treated stretch of water may be calculated to comprise some 1.86 million cubic metres or 410 million gallons. The 450 lb. of DDT thus added to 4,100 million lb. of water is equivalent to a concentration of 0.11 p.p.m. This dosage in 1 hr. 50 min. flow of water is equivalent to a dosage of 726 parsecs (0.11 p.p.m. multiplied by 6,600 seconds).

The treated water was observed from the air at 1.40 p.m. to have travelled four miles, and at 6.25 p.m. the solvent was detected by smell on the Blue Nile opposite Khartoum. A water sample taken at this point at 6.00 p.m. proved on analysis to contain 0.017 p.p.m. DDT,* while six further successive samples taken at hourly intervals as the river passed this point showed 0.003 p.p.m. DDT. The next morning (21st January) no DDT could be detected in the water at 11.30 a.m.

The larval and pupal population in the water at Khartoum was assessed on the evening of 20th January, after the main body of DDT had passed, by means of six plankton-net tows each of four minutes' duration, and compared with a similar pre-spray assessment made on 17th January. The population on the bottom was assessed on 21st January by six Peterson-dredge samples and compared with a similar pre-spray assessment also made on 17th January. The nets and dredges were of the same size as those described above, and the figures for the total larvae and pupae found were as follows:

		Larvae	Pupae
Pre-treatment	Plankton	23	11
	Bottom	212	10
Post-treatment	Plankton	16	11
	Bottom	216	7

It is evident that on the evening of the day on which treatment was applied, and on the following day, there was no effect on the numbers of midge larvae and pupae. The numbers of adults were likewise apparently unaffected, as shown by a comparison of the numbers (average of five stations) caught at Khartoum for the three nights after that of 20th January with the three nights before it, as follows:

January 17	41,690	January 21	74,130
18	11,220	22	26,920
19	60,260	23	100,000

The treatment of the river with DDT killed a number of fish of various species. Analyses by Burden (1956) of dead specimens revealed visceral DDT concentrations of 2.5 p.p.m. in *Labeo* sp. and 79 p.p.m. in *Synodontis schall*. Laboratory

* At this point, 10 miles downstream of the point treated, one might have expected a dilution of at least three times, that is, to a concentration of at most 0.04 p.p.m. (see Arnason & others, 1949). The water sample may have been taken just after the peak concentration had passed.

tests of the susceptibility of *Tilapia nilotica* had shown that this species could survive exposure to 0.2 p.p.m. DDT for three hours. The toxicity of the DDT in the river treatment may have been enhanced either by the detergent, as Burden suggested, or by the floating oil film, at least two miles long, the continuity of which ensured the contamination of all fish coming to the surface.

Spraying with DDT at Khartoum.

An area of 300 acres between Sharia el Gasr el Gamhouri and Sharia Gamaa was treated with DDT applied from an aircraft at a rate of 2.1 lb. per acre in the late afternoon of 23rd January 1956. The aircraft (an Auster) made 14 parallel runs at 60 ft. height along the long axis of 2.5 miles, and the spray consisted of equal parts of water and 25 per cent. DDT emulsion concentrate. The adult population showed no decrease that evening, but it was considerably reduced for the next 15 days (fig. 2).

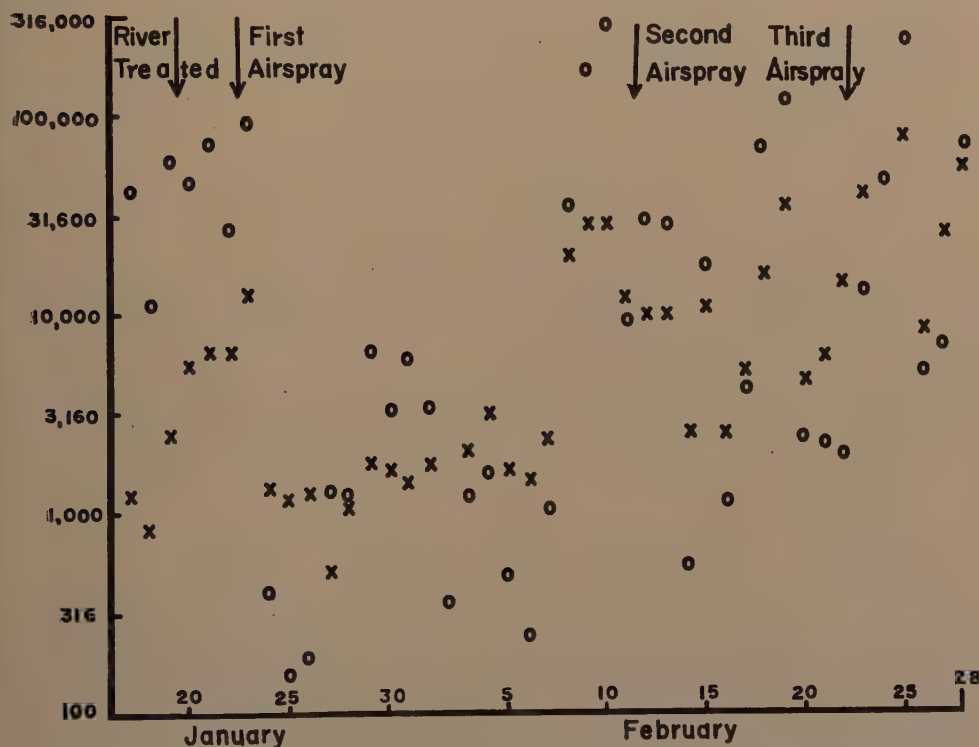


Fig. 2.—Populations of adult midges at Khartoum, 1956. Averages of 2-hour light-trap catches at: (i) 5 stations in Khartoum, O; (ii) 15 stations in Khartoum and Khartoum North, X.

A second airspraying was carried out in the morning and late afternoon of 12th February, covering 550 acres between Sharia el Gasr el Gamhouri and Sharia el Gamhouria (Sirdar Avenue, parallel to Gordon Avenue and one block further south) at a rate of 1.15 lb. per acre. A third airspray was applied in the late afternoon of 23rd February, covering the original 300 acres at a rate of 2.1 lb.

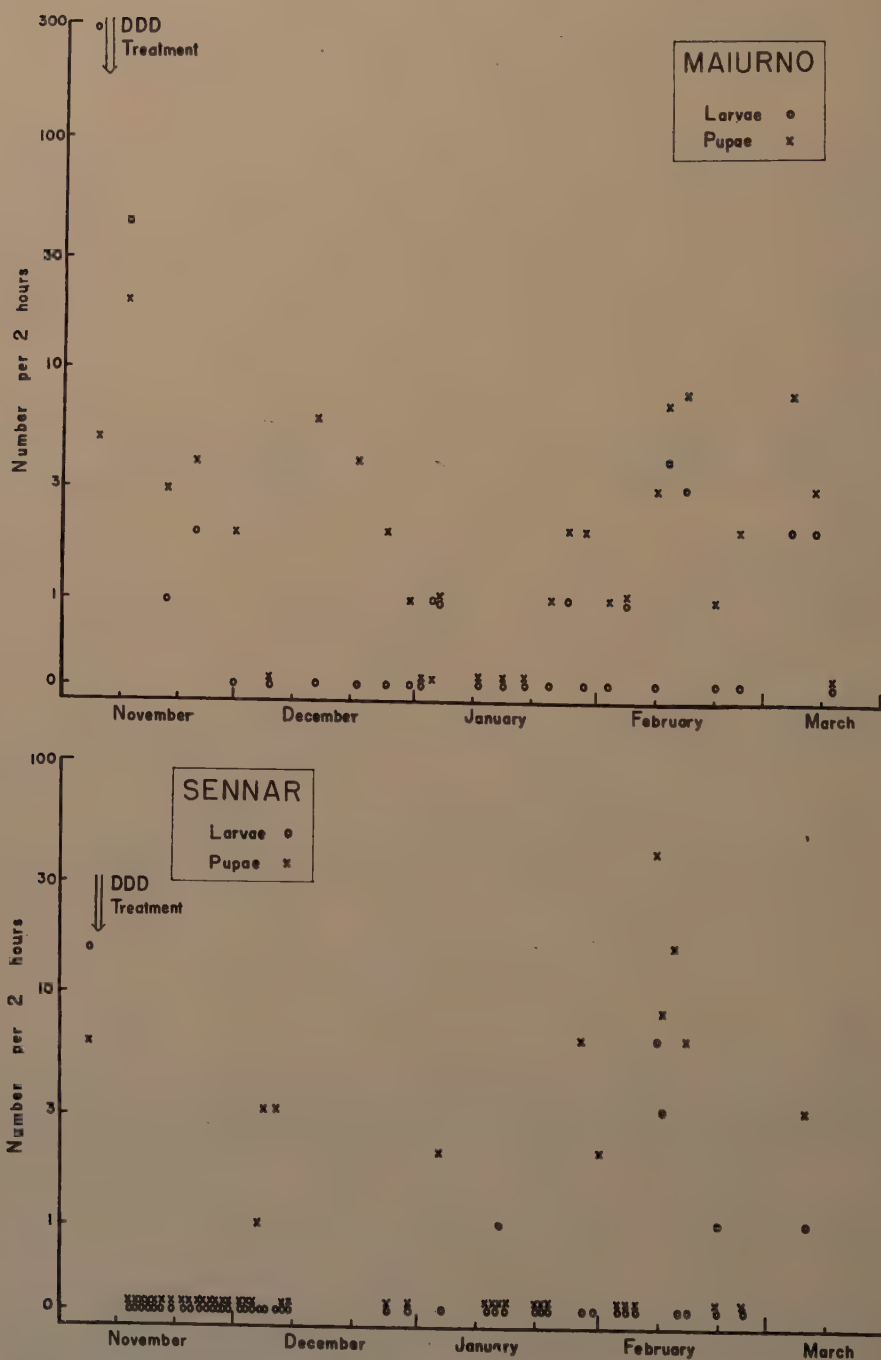


Fig. 3.—Larval and pupal populations at Maiurno and Sennar, 1957-58; numbers captured per 2 hr. by plankton-net (see p. 795).

per acre. Both these treatments failed to achieve control (fig. 2), the principal reason being that at the time of application the air was much warmer and more turbulent than at the time of the first treatment. It is considered that for success the spray should penetrate the crowns of the banyan trees and deposit DDT on their foliage. Tests with sprayed branches showed that the insecticide residue could kill adult midges by contact; continuous exposure induced the first knock-down after 1.5 hours and complete knockdown in 4.5 hours of all the flies exposed.

The heavily infested area centring on the Prime Minister's Office and extending to the river embankment was treated from the ground in the early morning of 19th March 1956. A 500-gallon cotton-sprayer and a 12-foot lance were used to apply a coarse spray of an emulsion containing 0.4 per cent. DDT to the 47 trees involved, at a rate of 0.5 to 1 lb. DDT per tree. Qualitative observations indicated that good control was obtained for the three following evenings, and that the population in this area remained lower than normal for the following 10 days.

Treatment of the Sennar Reservoir with DDD.

The principal operation against the midges of the Blue Nile was carried out in 1957. The midge larvae were attacked at the Sennar Reservoir, 150 miles upstream from Khartoum, since it was presumed that this was the ultimate source of the infestation. In order to avoid toxic hazard to fish, DDD (dichloro-diphenyl-dichloroethane) was substituted for DDT because DDD is much less toxic to fish and yet has proved very effective in controlling aquatic larvae of Nematocerosus Diptera (Lindquist, Roth & Walker, 1951). Moreover, instead of an oil-detergent formulation, an aqueous suspension of a wettable powder was used.*

A total of 500 lb. DDD was applied to the Blue Nile in the impounded section above Sennar on 6th and 7th November 1957. The suspension (made up at the rate of 1 lb. DDD (2 lb. wettable powder) per gallon of water) was emitted from an Auster aircraft equipped with a boom carrying a series of nozzles with No. 10 circular orifices. Each load of 50 gallons was emitted at approximately 8 gal. per min., allowing 6.25 minutes of emission time; during this time the aircraft, flying at 75 m.p.h., covered approximately 7.5 miles, or approximately $2\frac{1}{2}$ runs each three miles long. The flight lines ran parallel to the course of the impounded river. Three sections, each three miles long, were treated in the 30-mile stretch between Sennar and Suki (fig. 1) as follows:

I.	Marafa	200 gal. in 10 runs	10.07-13.30 hr., November 6
II.	N. of Suki	150 gal. in 7 runs	06.21-08.39 hr., November 7
III.	S. of Sennar	150 gal. in 6 runs	09.02-11.35 hr., November 7

Assessments made after the treatments showed that after 11th November larvae and pupae, particularly the former, became extremely rare at Maiurno, the east bay of which is three miles downstream of the treated section at Marafa, and remained so until mid-February (fig. 3). Near the dam at Sennar, larvae were recorded on one occasion only between the date of treatment and the 10th February 1958, and pupae were recorded only occasionally, and in small numbers (fig. 3). Assessments previously made at Sennar on 16th and 17th February 1956, had obtained five larvae and two pupae of Chironomids in nine plankton tows, and seven larvae in five bottom samples.

It may be concluded that the treatment of the reservoir with DDD effectively controlled the midge larvae in that area. This conclusion is fortified by the fact that the adult population in the Sennar area was exceptionally small in the winter of 1957-58.

* The insecticide was obtained as a 50 per cent. wettable powder from Rohm and Haas, Philadelphia, under the trade name of Rhothane.

Decisive results were not obtained in 1957-58 at Wad Medani, 60 miles down-river from Sennar. Although larvae were rare, pupae were abundant there from 10th November 1957 to 4th February 1958 (fig. 4). It is probable that this is the normal situation, although seasonal data from former years are not available. Since the adults remained abundant at Wad Medani in early 1958, it may be

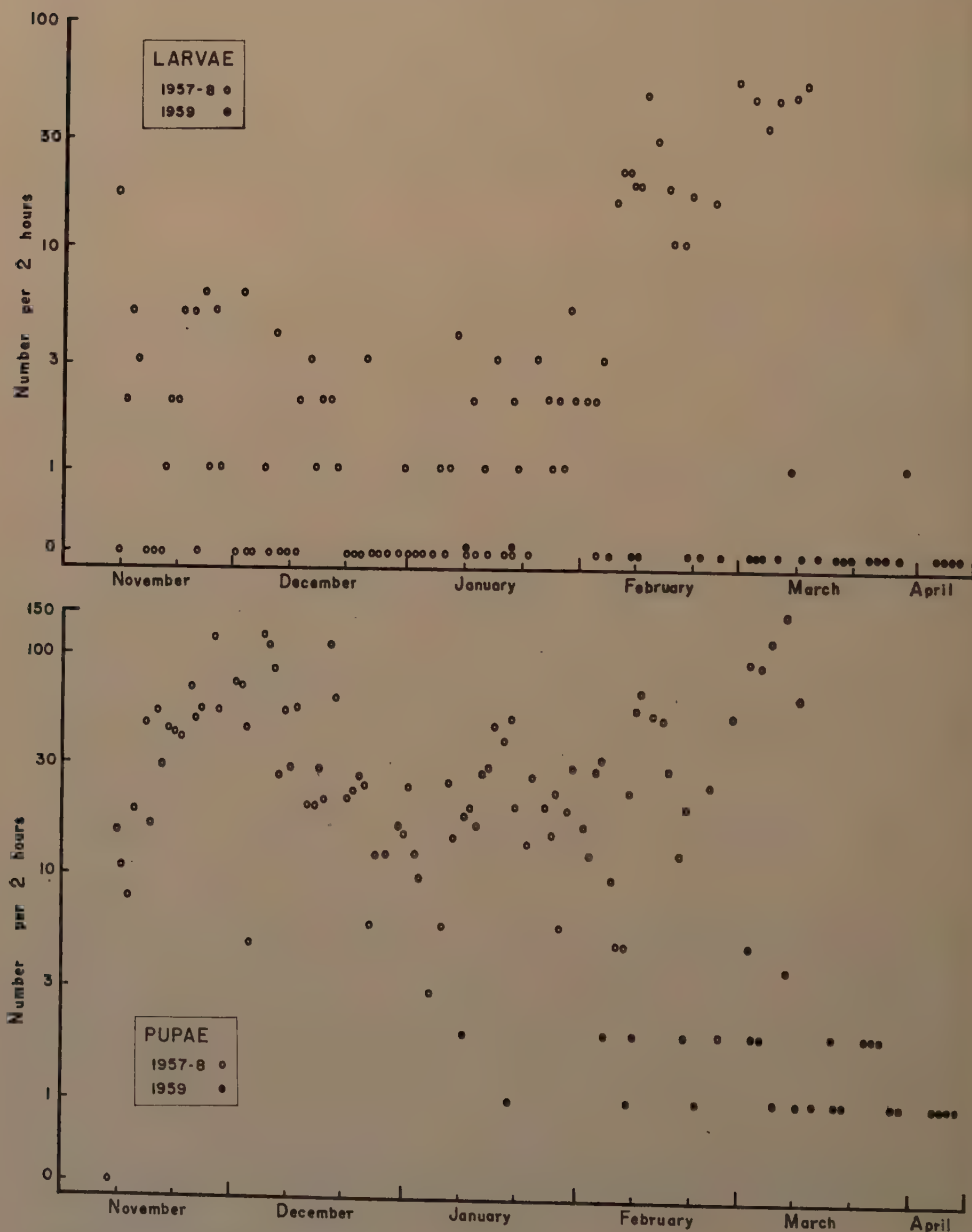


Fig. 4.—Larval and pupal populations at Wad Medani, 1957-58 and 1959; numbers captured per 2 hr. by plankton-net (see pp. 796-797).

concluded that the DDD treatment did not extend its effect for 60 miles downstream during the 1957-58 season.

During 1959, however, it became apparent that larval abundance had greatly decreased at Wad Medani. No larvae were found during January and February (Table I), and during March only two of the 15 samples showed any larvae, each containing a single specimen (fig. 4). The average monthly pupal population counts did not exceed two for any of the three months in 1959, as compared with averages of 23, 30 and 104 in 1958 (Table I).

TABLE I.

Larval and pupal populations at Wad Medani and Khartoum. Arithmetic averages of nightly catches in each month (adjusted to 2-hours' sampling time).

WAD MEDANI	1952*		1958		1959	
	Larvae	Pupae	Larvae	Pupae	Larvae	Pupae
January	—	—	1.2	23	0	1.5
February	—	—	17	30	0	1.7
March	34	115	44	104	0.2	1.9

KHARTOUM	1951*		1956†		1958		1959	
	Larvae	Pupae	Larvae	Pupae	Larvae	Pupae	Larvae	Pupae
January	—	—	98	55	35	29	0	0
February	312	120	—	—	59	18	0	4.4
March	—	—	—	—	24	35	0.5	3.2

* Data from Lewis (1957, p. 166 and fig. 5).

† Based on mean of data on p. 792.

During 1959 a marked change became apparent also at Khartoum. Here the larval and pupal populations in 1958 had remained high (fig. 5), though perhaps not as high as those reported by Lewis for 1951 and later found in 1956 (Table I). But in 1959 the larval population was nil in January and February, and only one out of six samples in March was positive, containing three larvae (fig. 5). Pupae were not found in January, and although they were present in all but three of the samples taken in February-March, the numbers were much less than in 1958.

The adult population at Khartoum in 1959 was notably low. The assessment counts in February and March were only about one-eighth of those obtained in 1958 (Table II). Since the populations of 1958, like those of 1956, could be considered to have been to some degree subnormal by reason of preceding insecticidal operations, the 1959 populations were compared with figures for 1951 and 1952 obtained by Lewis, Henry & Grindley (1954). These were originally plotted on an arithmetic scale, but they are here shown after conversion to a logarithmic scale of abundance (fig. 6); no other correction factor was applied, although these workers used a shorter assessment period and a smaller dish in the light trap (Grindley, 1952), and also dried the flies for a much longer period (.5 hr. at 50°C.), the final weight being about one-third of that in the present experiments. When the average figures computed for the months of February,

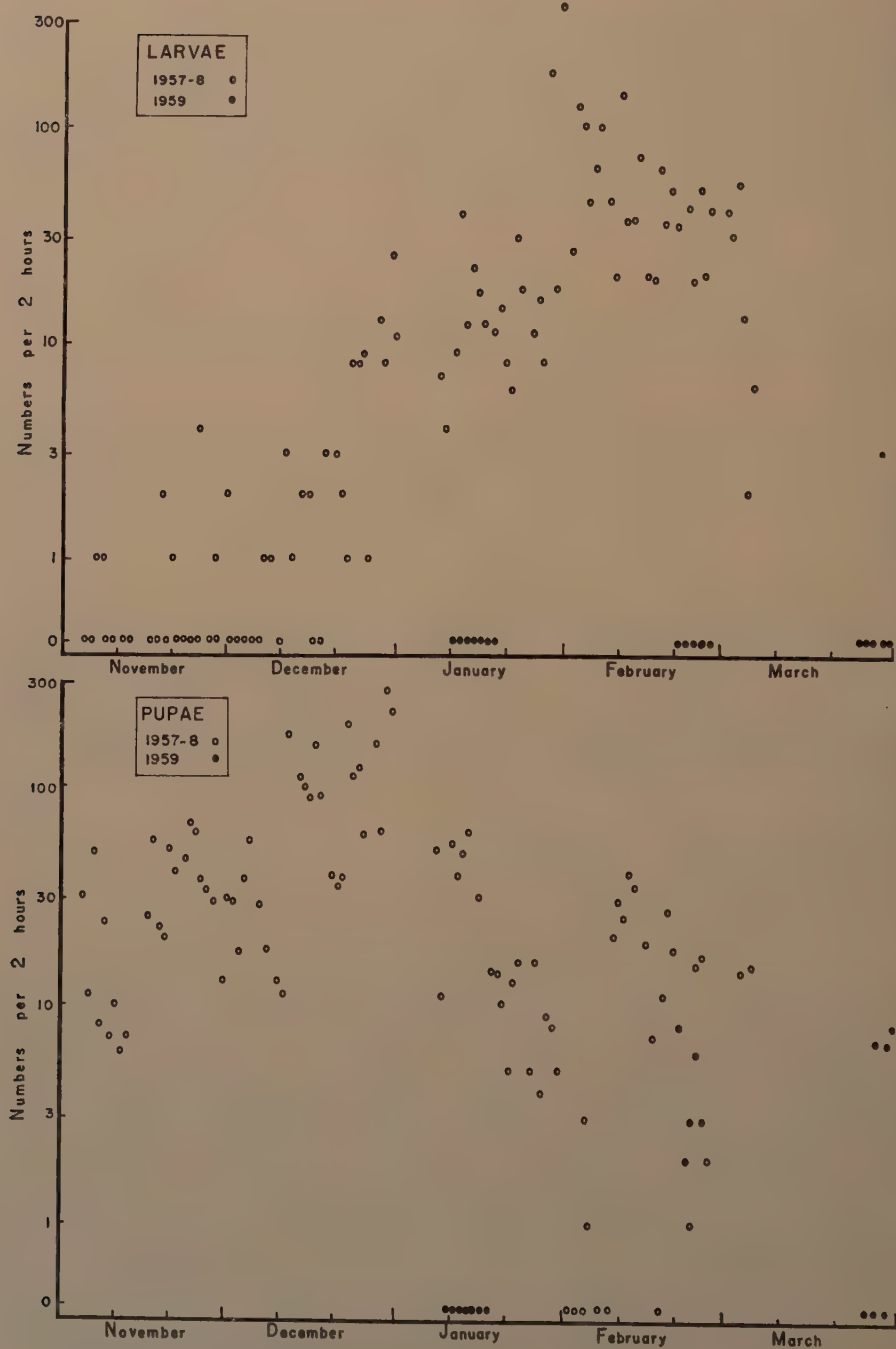


Fig. 5.—Larval and pupal populations at Khartoum, 1957-58 and 1959; numbers captured per 2 hr. by plankton-net (see p. 797). The numbers of pupae for 1st-6th March 1958 were as follows: 54, 27, 70, 14, 32, 15. Only 14 and 15 are shown, the others having been omitted in error. The three entries for pupae at 0 in March 1959 should have been plotted at 1.

March and April of 1951 and 1952 are compared with those for 1959 (Table II), it becomes evident that the infestation of midges in 1959 had fallen to a level that was only 0.6-5.0 per cent. of the former intensity. Qualitative observations indicate that the adult population remained low throughout the season of 1959-60.

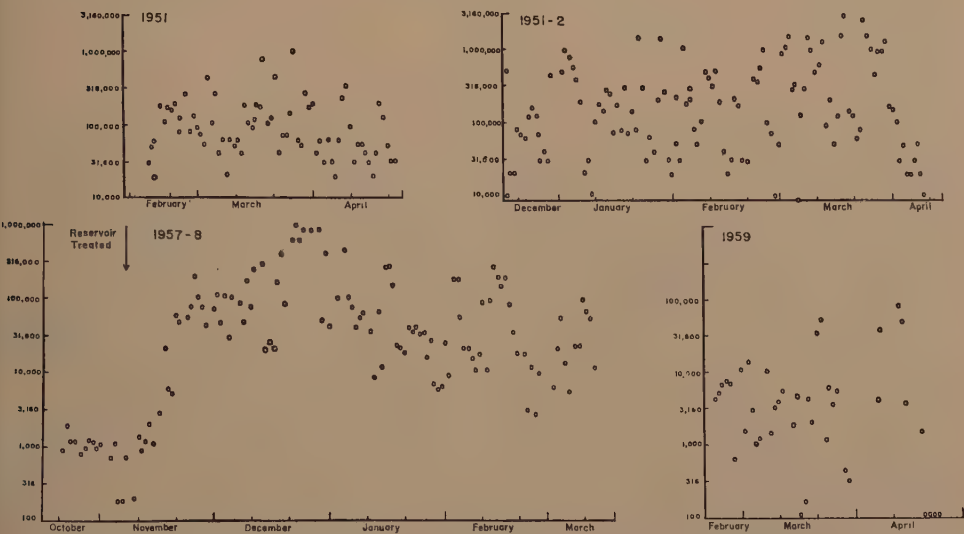


Fig. 6.—Populations of adult midges at Khartoum, 1951, 1951-52, 1957-58 and 1959.

Unfortunately there is at present no means of ascertaining how far natural fluctuations are responsible for this decisive and unprecedented reduction of population density. The uniqueness and size of the Blue Nile makes it impossible to adduce an untreated situation as a check for comparison. The same difficulty

TABLE II.

Adult populations at Khartoum. Geometric means of nightly catches in each month.

	1951*	1952*	1956	1958	1959
January	—	141300	6200	40700	—
February	95500	128800	8500	35500	4800
March	109600	380200	—	20400	2400
April	52500	29500	—	—	560

* Data from Lewis, Henry & Grindley (1954).

in logic was presented in a similar treatment of the South Saskatchewan river with DDT (Arnason & others, 1949), which was followed by disappearance of *Simulium* larvae for a distance of 90 miles downstream. The delay interposed between application and population reduction, amounting to one year at Wad Medani, which is only 70 miles downstream from the area of application, poses an especially difficult question. A possible explanation is that populations

originate as eggs laid many miles upriver, and that the net result of the treatment was to remove the source of that population in the Sennar reservoir. In fact, this was the intention in aiming the final operation at the presumed source of midges in the Blue Nile. The impoundment at Sennar extends its effect for nearly 20 miles upstream, and thus the application could not remove all sources of population above the treated area; such sources may be responsible for the reappearance of the small numbers of larvae and pupae noted in the reservoir three months after its treatment.

Summary.

In 1956 and 1957, tests were made in the Sudan Republic of four methods of applying insecticides for the control of heavy infestations of midges, particularly *Tanytarsus lewisi* Freeman, which breed in the Blue Nile. During the winter season, the adults occur in myriads in areas adjacent to the river in Khartoum and similar localities, resting in trees and shrubs by day and being attracted to artificial lights after dusk. 444 66, 45 93 DE

An emulsion containing 0.4 per cent. DDT applied from the ground to shade-trees in Khartoum at the rate of 0.5–1.0 lb. DDT per tree achieved local control of the midges for three days and detectable reduction for 10 days. An emulsion containing 12.5 per cent. DDT applied from an aircraft to the wooded river-frontage at Khartoum at 2.1 lb. per acre reduced the numbers of adult midges for the next 15 days, but subsequent applications under conditions of greater air turbulence were ineffective.

The application of DDT as a larvicide in oil solution from aircraft to the river 10 miles above Khartoum, at a concentration approximately equivalent to 0.1 p.p.m. in 2 hours' riverflow, did not appear to reduce the numbers of adults or immature stages at Khartoum, and was followed by some mortality of fish.

The application of 500 lb. DDD as a larvicide in 500 gal. of a wettable-powder suspension sprayed from aircraft on 6th–7th November 1957 to three 3-mile sections of the Blue Nile reservoir in a 30-mile stretch upstream of the Sennar dam, 150 miles above Khartoum and 60 miles above Wad Medani, was followed by exceptionally low densities of larvae and adults at Sennar in early 1958 and at Wad Medani and Khartoum in early 1959.

Acknowledgements.

This programme was initiated by Dr. A. A. Zaki, Director of Medical Services, and Dr. Ali Kheir, Deputy Director of Medical Services, Ministry of Health, Republic of Sudan, to which the authors are indebted for facilities and the supply of labour. The determinations of DDT in the water were made by Dr. E. H. W. J. Burden, former Government Analyst, who assisted in many other ways in 1956 and 1957. Sayed Riad Mansour, Government Analyst, directed the assessments of the adults during 1957–8. Larval assessments were largely supervised by Ahmed Effendi Abdel Rahman Bereir, Medical Entomological Section, Gezira Research Station, and his outstanding service is greatly appreciated. Invaluable assistance in setting up the larval assessment was provided by Dr. J. Rzoska, University of Khartoum. Mr. A. E. Hoffstede, Game and Fisheries Department, assisted with the tests of toxicity to fish. Mr. J. S. Hewitt and Mr. A. J. Jones, Fisons Pest Control (Sudan) Ltd., assisted in the operational arrangements in 1957 and 1958, and Mr. W. van Mierlo and Mr. J. Donaghy piloted the aircraft in 1956 and 1957, respectively. Finally, the authors are greatly indebted to Dr. D. J. Lewis, whose studies on the complicated biology of these little-known insects, advice, and comments on this paper in draft, have all been invaluable.

References.

- ARNASON, A. P., BROWN, A. W. A., FREDEEN, F. J. H., HOPEWELL, W. W. & REMPEL, J. G. (1949). Experiments in the control of *Simulium arcticum* Malloch by means of DDT in the Saskatchewan river.—*Sci. Agric.* **29** pp. 527–537.
- BURDEN, E. H. W. J. (1956). A case of DDT poisoning in fish.—*Nature, Lond.* **178** pp. 546–547.
- GRINDLEY, D. N. (1952). The composition of the body fat of small green Chironomids.—*J. exp. Biol.* **29** pp. 440–444.
- LEWIS, D. J. (1957). Observations on Chironomidae at Khartoum.—*Bull. ent. Res.* **48** pp. 155–184.
- LEWIS, D. J., HENRY, A. J. & GRINDLEY, D. N. (1954). Daily changes in the numbers of Chironomid midges at Khartoum.—*Proc. R. ent. Soc. Lond.* (A) **29** pp. 124–128.
- LINDQUIST, A. W., ROTH, A. R. & WALKER, J. R. (1951). Control of the Clear Lake gnat in California.—*J. econ. Ent.* **44** pp. 572–577.

OBSERVATIONS ON EMERGENCE AND LIFE-SPAN OF WHEAT BULB
FLY, *LEPTOHYLEMYIA COARCTATA* (FALL.), UNDER
FIELD-CAGE CONDITIONS.

E.M.M.

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In 1956, emergence and life-span of the adult wheat bulb fly, *Leptohylemyia coarctata* (Fall.) were studied by observations on the population of an area of infested wheat enclosed by a large cage of mosquito-netting (Dobson, Stephenson & Lofly, 1958). The enclosed area was searched daily and all newly emerged flies were caught, recorded, marked according to date of capture and liberated in the cage. The survivors were recaptured and reliberated regularly and, from the data obtained, the rate of population decline was estimated. The life-span of individual flies could not, however, be observed directly.

In 1957 and 1958, the work was repeated with improved techniques which reduced experimental hazards and enabled individual life-span to be estimated. As before, the site chosen was Pennell's Piece, a small field adjoining the classical wheat field, Broadbalk, at Rothamsted.

Technique.

The method used to study emergence was the same in all three years. Populations of flies were sparse during 1957 and 1958, and it had been hoped to supplement the natural emergence in the cage with flies obtained from the next field. This proved impossible as local micro-climatic differences had a marked effect (see p. 808). Flies from outside the cage that emerged on suitable dates were, however, used in the cage for the other studies.

The main criticisms of the method of studying population decline used in 1956 are that life-span could not be directly measured and that both flies and wheat suffered from excessive handling. In subsequent experiments the flies were marked so as to be distinguishable individually rather than according to emergence date only and this enabled the histories of individual flies to be studied. The use of individual marks also obviated the need to catch the flies during 'recapturing', because all that was needed was to record the presence of particular individuals. In 1958, the technique was further improved by arranging the experiment so that observations could be made without touching either wheat or flies. This had the advantage that notes on the activities, natural positions and postures of undisturbed flies could be made during routine observations on marked flies.

The 1957 experiment.

The cage used in 1956 (24 ft. long, 12 ft. wide and 6 ft. high) was used again and six paths were cut through the wheat, two lengthwise and four across, to give access to all parts of the enclosure. Both newly emerged and marked flies were searched for daily, the wheat being agitated continuously to make them fly up. The sex and identity of marked flies could be determined by observation from a distance of about 18 inches, so they were usually recorded without being handled and only unmarked flies were actually caught. On certain 'test' days, however, at about ten-day intervals, an attempt was made to catch the entire population

* Now at Zoology Department, Glasgow University.

so that the adequacy of the routine technique could be checked. Usually two people searched independently at the same time, but on some days there was only one person. Each search was continued until it seemed likely that no further flies would be found; the time needed varied between one and three hours, depending on numbers.

Preliminary sampling of immature stages indicated that the natural population was much lower than in 1956, and, to increase the numbers for the study of life-span, many newly emerged flies bred out of pupae obtained from Broadbalk were marked and introduced into the cage.

Nitrocellulose lacquers in five basic colours,* white, violet, blue, red and yellow were used for marking, with two extra shades, orange and green, prepared by mixing yellow with red and blue, respectively. Violet and blue, being transparent, appeared dark when used alone, so they were mixed with a high proportion of white to make them opaque.

These lacquers seemed as durable and as resistant to fading as the artists' oil colours used previously, and were preferred because they dried quickly and did not leave a spreading stain on the integument. Three paint spots, arranged in a triangle, were placed on the dorsum of the thorax of each fly, and with seven colours, 343 (*i.e.*, 7^3) different combinations were available. Only three-spot combinations were used, so that all flies carried approximately equal loads. As before, to facilitate marking, the flies were made comatose by chilling, and after marking they were placed in ventilated containers which were opened in the cage. Individuals later found dead in these containers were regarded as marking casualties and were not included.

The 1958 experiment.

The cage was doubled in size to 24 ft. \times 24 ft. \times 6 ft. high, and the enclosed wheat was divided into sixteen 4-ft. square plots separated and surrounded by paths. As in 1957, the natural population was supplemented by introduced flies and individual marks were used. From the 1957 results, it was suspected that two of the lacquers (yellow and violet) were harmful to the flies, so that only shades mixed from the basic colours blue, red and white were used. Five shades, blue (blue + white), red, white, pink (red + white) and brown (blue + red + white) were available and, by using three different configurations of three-spot combinations, 375 individuals of each sex could be distinguished. The marking technique was standardised by keeping the flies first at 5°C. for 15 minutes, then at 0°C. for 30 minutes (during which time they were marked) and then at 5°C. for a further 15 minutes. Flies were only partially incapacitated by this treatment, and it was hoped that possible harmful effects of sudden changes of temperature would be lessened.

Searches were made daily and, as in 1957, only unmarked flies were captured. At first, while the flies were still few, the wheat was agitated by hand, but after a few days all searching was made without touching either flies or wheat. Every part of the enclosed area was inspected once only during each day's searching, and, to facilitate finding the flies, the crop was kept free from excessive growth of weeds. This method of searching was less efficient (Efficiency = $\frac{\text{No. of flies recaptured}}{\text{No. available for recapture}}$) than the methods used previously but it had two advantages. First, observations on the behaviour and distribution of relatively undisturbed flies could be made, and secondly, counts on different days and under different weather conditions could be compared.

* I.C.I. Necol serial numbers: (1) White—FO. 56-101; (2) Heliotrope—FO. 56/CW/01065 (*i.e.*, violet); (3) Ultra Blue—FO. 56/CW/01066; (4) Scarlet—FR. 56/9920 (*i.e.*, red); (5) Golden Yellow—FR. 56-456.

Depending on the number of flies present, searching took between 35 minutes and $4\frac{1}{2}$ hours each day.

Effects of chilling and marking.

Some effects of chilling the flies and of marking them with artists' oil paint were discussed by Dobson, Stephenson & Lofty (1958). Two spots of paint were apparently not more harmful than one, and it was decided in 1957 that it would be a fair risk to use three spots, the least number needed to give a reasonable range of different combinations. Care was taken, of course, to ensure that the paint spots were small and that they adhered securely to the cuticle of the fly.

In 1957, when nitrocellulose lacquers were substituted for oil paints, the recapture figures showed that higher proportions of both sexes died 'prematurely', that is, within five days of emergence, than would have been expected with random mortality. No particular marking colour appeared to be lethal but the proportion of short-lived individuals was greater amongst those bearing yellow or violet spots than amongst the others. The effect of different colours of paint on the life-spans of the flies was tested statistically. This test was based, for each sex, on 133 different sets of three spots arranged in a triangle, each set comprising not more than two of the seven colours, and each colour thus appearing in 37 different sets. Table I summarises the results: the figures for yellow and for violet suggested

TABLE I.

Survival of flies marked with given colours, 1957.

Colour	Numbers surviving					
	5 days or less			6 days or more		
	♂	♀	Total	♂	♀	Total
White	10	10	20	27	27	54
Red	6	11	17	31	26	57
Orange	8	14	22	29	23	52
Yellow	21	15	36	16	22	38
Green	16	11	27	21	26	47
Blue	13	7	20	24	30	54
Violet	19	11	30	18	26	44
	93	79	172	166	180	346

that these colours were harmful, and those for green supported the suspicion regarding yellow. Significance tests (Table II) appeared to confirm these doubts, so it was decided not to use yellow and violet in the 1958 experiment and to test all the colours in the laboratory when flies became available.

In these laboratory tests, 44 sets of newly emerged flies were observed. Each set consisted of 7 males and 7 females kept in a lamp glass and provided with condensed milk, honey and meat extract as food (*cf.* Bardner & Kenten, 1957) and the following treatments were applied. Five pairs of flies were chilled (using 1958 standard procedure) and marked with a single spot of one of the five colours to be tested, *i.e.*, white, yellow, blue, red and violet; one pair was chilled only and one control pair was neither marked nor chilled. The flies were kept at 20°C. and 45 per cent. relative humidity and subjected to a cycle of 16 hours light (provided by fluorescent tubes) and 8 hours darkness. All sets were examined daily and dead flies were removed. Accidental losses were few. Under these

conditions flies were fairly short-lived, the mean life-span being 8.8 days for males and 24.0 days for females.

The yellow and violet paint seemed no more harmful than the others in this experiment, but females marked with white showed a slightly higher mortality than all other categories for the first 20 days (difference between white and controls significant at $P=0.05$ on 11th, 12th and 13th days). However, the proportions surviving 21 days or more (*i.e.*, approaching maturity) and the expectation of life, even of those marked with white, were not affected.

TABLE II.

Significance tests to show effects of different marking colours, 1957.

Flies marked with	Premature deaths			Survived 6 or more days Total	Comparison with safe colours (white, red & blue) χ^2 test
	♂	♀	Total		
White, red & blue only ..	3	4	7	35	—
Orange and/or green but excluding yellow and/or violet	11	14	25	63	$\chi^2 = 1.53$ $0.30 > P > 0.20$
With yellow	21	15	36	38	$\chi^2 = 10.44$ $P < 0.01$
With violet	19	11	30	44	$\chi^2 = 5.97$ $0.02 > P > 0.01$

Among the males, of which 95 per cent. had died by the 14th day, the groups of differently coloured flies all had similar mortality, but both chilling and painting appeared to be harmful and resulted in higher mortality from the 3rd to the 14th days. Comparing the aggregate of marked and chilled males with the controls, the differences in mortality were significant at $P=0.05$ for the 5th and 6th days and at $P=0.01$ for the 7th–11th days. It was concluded, therefore, that the adult males, which are less robust than the females, are more likely to be injured by marking and chilling but that no particular colours were especially harmful under the conditions of the experiment. The mean life-spans of the three groups of males, chilled and marked, chilled only, and control, were 8.38, 9.36 and 10.19 days, respectively.

A possible cause of the premature mortality observed in 1957 was that some batches of flies might have been subjected to unsuitable conditions during or after marking. For example, from 16th to 19th June, there was a period of hot weather (the daily mean temperature on bare grass being 20°C. or more) and there was an abnormally high premature mortality of flies emerging on these days and an especially high premature mortality of flies marked with yellow or violet (Table III). It seems likely that the sudden chilling by exposing to -5°C . may have been more harmful when the flies were at a high temperature at the outset. During the cooler weather (daily mean temperature less than 20°C.), *i.e.*, before 16th and after 19th June, newly emerged flies marked with yellow or violet still tended to die prematurely but the differences were less and were not significant statistically.

The need for care in marking is obvious, and during a separate field experiment in 1958, in which many flies had to be marked quickly, many individuals were later found to be unable to fly. The mass of paint carried seemed not to be

the deciding factor because some of the incapacitated flies had very small spots whereas others which could fly had large ones. As a result of these observations the flies in the cage were tested for their ability to fly; of 166 males and 221 females, 11 and 17, respectively, could not fly. In both sexes the mean life-span of these disabled individuals was only three-fourths that of normal flies.

TABLE III.

Significance tests showing effects of the marking colours under different weather conditions.

Fly material	Weather condition, or colours used	Number of flies emerged	Number dying within 5 days	χ^2	P
All flies that emerged during periods specified	Hot period 16-19.vi.	178	77	22.30	<0.001
	Cooler periods 6-15.vi. & 20-27.vi.	160	30		
Males as above	Hot period	93	44	14.92	<0.001
	Cooler periods	85	16		
Females as above	Hot period	85	33	6.83	<0.01 >0.001
	Cooler periods	75	14		
All flies that emerged during hot period	Marked with safe colours	84	26	8.89	<0.01 >0.001
	Marked with yellow and/or violet	94	51		
Males as above	Safe colours	39	13	4.34	<0.05 >0.02
	Yellow and/or violet	54	31		
Females as above	Safe colours	45	13	3.15	<0.10 >0.05
	Yellow and/or violet	40	20		
All flies that emerged during cooler periods	Safe colours	91	14	1.11	<0.30 >0.20
	Yellow and/or violet	69	16		
Males as above	Safe colours	54	7	3.45	<0.10 >0.05
	Yellow and/or violet	31	10		
Females as above	Safe colours	37	7	0.003	>0.95
	Yellow and/or violet	38	6		

Results.

Emergence.

In 1956, all the flies under observation were those that had emerged naturally from the infested wheat in the cage. In 1957 and 1958, because populations were low, attempts were made to increase the numbers of flies in the cage by taking pupae from Broadbalk, at a point about 250 yards from the cage, and allowing them to emerge from pots of peaty loam sunk to soil level in the crop near the

cage. This plan failed because the emergence dates of the two populations differed greatly. Table IV summarises results obtained from three different populations observed during 1958; (a) the natural population of Pennell's, (b) flies derived from pupae obtained from Broadbalk between 12th and 27th May and immediately transferred to Pennell's, and (c) pupae obtained from Broadbalk

TABLE IV.

Emergence dates of flies in 1958.

Source of flies		Date of emergence of		
		First flies	50%	Last flies
(a) Natural infestation of cage	♂	17 June	2 July	21 July
	♀	17 June	8 July	22 July
(b) Pupae obtained in Broadbalk but kept by cage	♂	12 June	28 June	19 July
	♀	19 June	30 June	20 July
(c) Pupae obtained and kept in Broadbalk ..	♂	13 June	20 June	1 July
	♀	14 June	24 June	5 July

but kept there (data kindly supplied by Dr. D. B. Long). The differences observed probably reflect micro-climatic differences between the two sites. The crop on Broadbalk was much less advanced than that on Pennell's so that the soil received more solar radiation and was warmer, and also the soil of Broadbalk was drier than that of Pennell's.

The emergence data of the natural populations of the cage site for 1956, 1957 and 1958 and also the temperature summations in degree-days above 42°F. (5.6°C.) from 1st January are shown in fig. 1. Consistently, males appeared before females, but there were considerable differences from year to year. The immature stages occur in the soil and plants and, as the eggs are fully developed in autumn but do not hatch until after the frosts in early spring, temperature during post-embryonic development is probably the most important factor influencing date of emergence. There is, as yet, no precise knowledge of the relation between temperature and development in wheat bulb fly, but the flies emerged latest in 1956, when the spring was coldest, and earliest in 1957, when it was warmest. Temperature summation is quoted merely to make a broad comparison of the three seasons, and the values given must not be regarded as estimates of the thermal requirements of developing flies.

Life-span of flies.

As the life-span of individual flies could not be measured in 1956, the half-life of the population was estimated indirectly on the assumption that, after the losses caused by marking, mortality was essentially random. In 1957 and 1958, when individual marks were used, direct estimates were possible and it became clear that the 1956 estimates of half-life were too low. The reasons for this can be illustrated by an example. On 28th June 1958, 23 male flies were marked and released in the cage; the recapture data can be expressed in three different ways: (a) the actual numbers observed on the following days; (b) the actual numbers known, from later observations on individually marked flies, to have been alive on that day; or (c) the best estimate of the minimum numbers alive on each day if all had been marked according to emergence date only so that they were not

recognisable individually. The numerical values for recaptures expressed in these ways are given below.

	June										July										
	28	29	30	1	2	3	4	5	6	7	8	9	10	11	12	13	. . .	28			
(a)	23	8	6	9	8	6	10	6	12	14	5	6	9	10	5	4	. . .	8			
(b)	23	23	23	23	22	22	22	22	21	21	20	20	19	19	19	19	. . .	14			
(c)	23	14	14	14	14	14	14	14	14	14	10	10	10	10	8	8	. . .	8			

Method (c) gives a low estimate of the numbers surviving and it is clear that the sharp drop in numbers between marking and first observation, formerly thought to be an effect of marking, is largely an artefact of the technique.

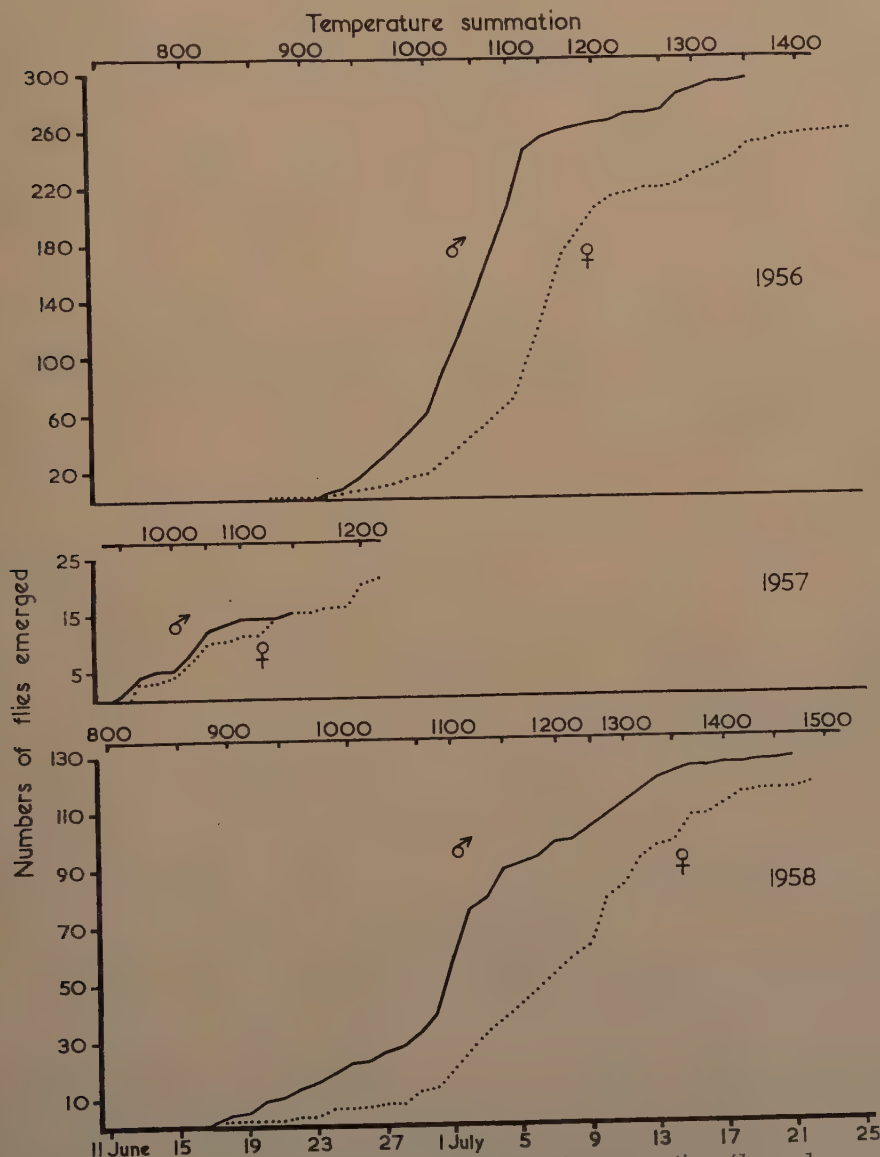


Fig. 1.—Accumulated emergence figures and temperature summations (degree-days above 42°F.) for 1956, 1957 and 1958.

The data for the three years (Table V) show that as the technique was improved so the apparent and real premature mortality decreased and the estimated half-life increased. For this reason, therefore, only the 1958 data will be dealt with in detail.

TABLE V.

Premature mortality and half-lives of flies in 1956, 1957 and 1958.

		% mortality				Estimated half-life of population	
		1 day		5 days		(days)	
		♂	♀	♂	♀	♂	♀
1956	Marking casualties	31.5	31.9				
	Survivors of marking	9.8	5.7	40.2	27.5	7.3	11.1
1957		2.2	2.2	12.5	16.4	12.7	18.0
1958		2.4	2.1	9.3	6.0	33.4	31.4

The frequency distribution of life-span for male and female flies in 1958 is shown in fig. 2. Only a small proportion of flies was actually found dead (7.6% males, 3.6% females) so, in general, life-span had to be taken as the number of days, including those when first and when last seen, that flies were known to have

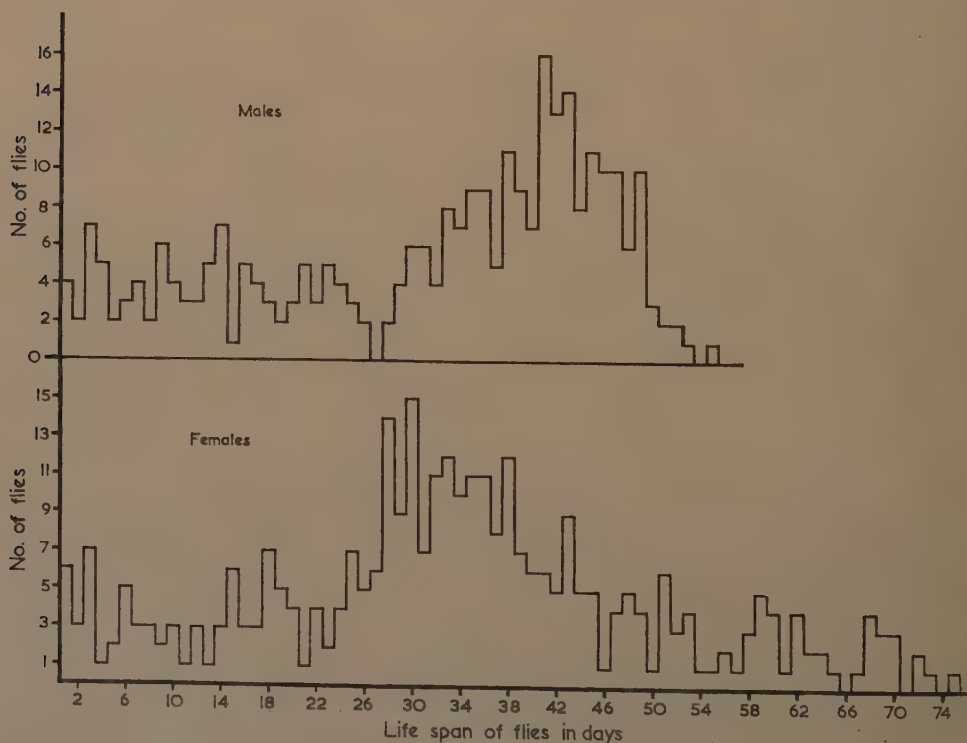


Fig. 2.—Frequency distribution of life-span amongst male and female flies observed in 1958.

lived. It will, of course, be appreciated that this under-estimates the true life-span because the disappearance of a fly does not imply its immediate death. It was obvious that flies often lived for some time after the last appearance recorded during routine searching because on certain days, when prolonged observations were made in connection with studies of behaviour, individuals were found which, according to the standard records, had disappeared and had been presumed dead. As will be shown later, a correction to allow for the difference between observed and true life-span can be calculated.

The frequency distributions of life-span for the two sexes are quite different. Deaths of males were relatively infrequent during the first 4½ weeks, amounting to a mean daily mortality of 1.3 per cent. of the total population. Mortality then increased to a maximum at about 6 weeks and after 8 weeks all were dead. Among females mortality was low during the first four weeks (mean of 1.1% per day), increased from 4 weeks to 6 weeks (2.9% per day) and then decreased again (0.8% per day) until all were dead in the 11th week.

Many of the mature females apparently survive for some considerable time, whereas males die off soon after reaching maturity. This difference is illustrated in fig. 3 which shows the number of flies more than 20 days old (and therefore

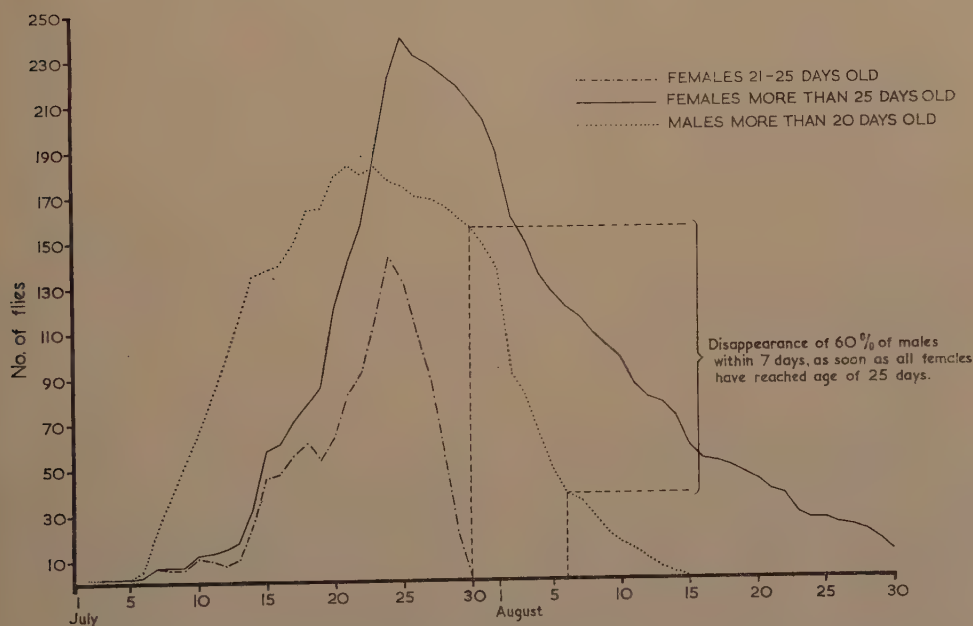


Fig. 3.—Number of flies more than 20 days old present in cage on each day (1958).

approaching maturity) in the cage on each day. Mature males and females co-existed for a while, but then the male population decreased by more than 60 per cent. in one week, at a time when all the females were more than 25 days old. The female population decreased during this time by less than 35 per cent. The observed life-spans of males and females arranged according to date of

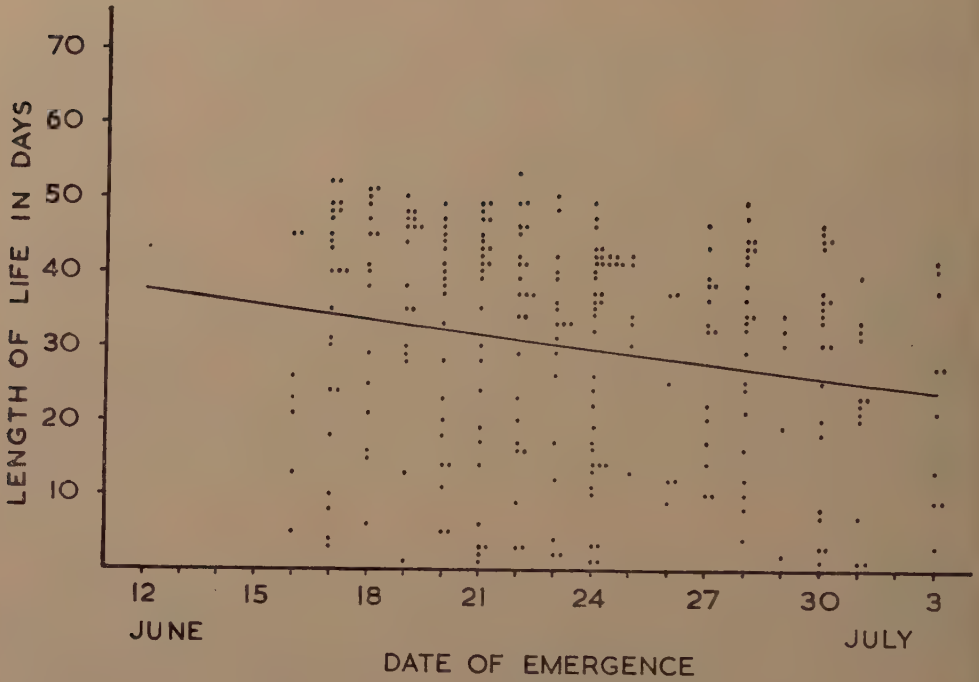


Fig. 4.—Observed life-spans of male flies in 1958.

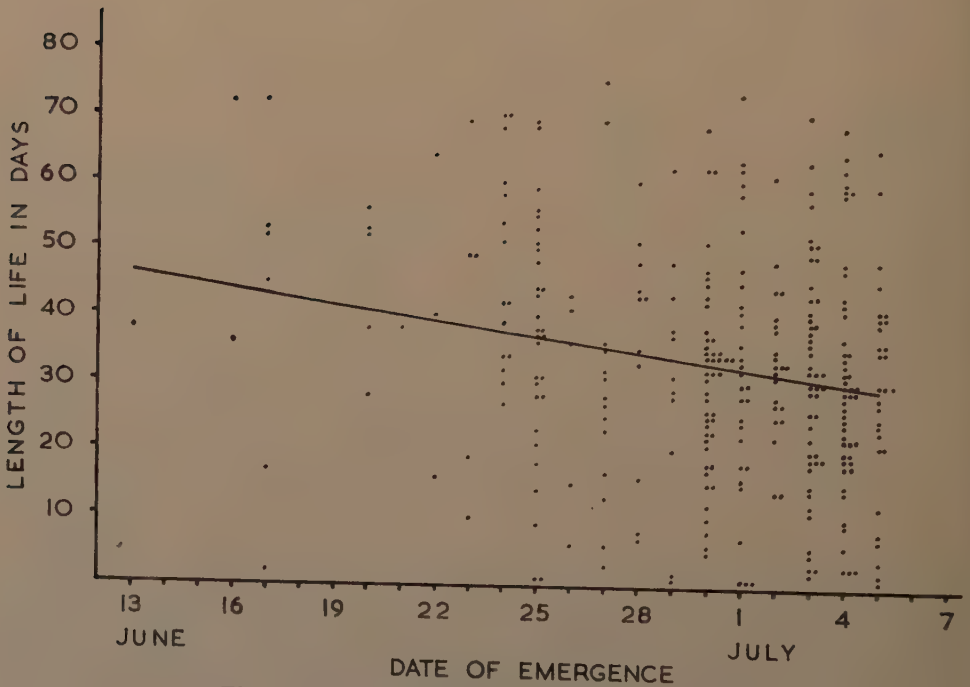


Fig. 5.—Observed life-spans of female flies in 1958.

emergence are shown in figs. 4 and 5. In both sexes, flies that emerged earlier in the season tended to live longer than those that emerged later. The regression lines shown have the equations:—

for males with mean life-span (\bar{y}) of 30.1 days

$$\hat{y} = 38.04 - 0.64x$$

for females with mean life-span (\bar{y}) of 33.2 days

$$\hat{y} = 47.96 - 0.82x$$

where $x=1, 2, 3$, etc. corresponds to the 1st, 2nd, 3rd . . . day of the emergence period for each sex. $x=0$ therefore corresponds to 11th June for males and 12th June for females. The standard errors of the regression coefficients, ± 0.19 for males and ± 0.21 for females show that both coefficients differ significantly from zero ($P < 0.001$). This reduced expectation of life of late-emerging flies was also observed in the females of the 1957 experiment but not in the males. The 1957 data are, however, less reliable because of the high premature mortality and inferior technique.

By 5th June 1958, it was decided that further additions to the already large population of marked flies in the cage would interfere with efficient note-taking, and the regression for the female expectation of life on time is therefore based on an incomplete emergence range. This is unfortunate as there is no way of knowing whether the relation implied by the regression would have continued. There are, however, three possible reasons for the decreased life expectation observed in later emerged flies. First, flies that emerged later may have tended to be, intrinsically, less long-lived than those that emerged earlier. This, however, appears unlikely because no such trend was noticed in the data for the laboratory tests on marked flies, in which over 300 individuals of each sex emerging during a period of 16 days were kept in a constant environment. Secondly, there may have been a progressive change in the environment, such as the ripening and drying of the crop gradually diminishing the food supply, or thirdly, there may have been a build-up of predators and disease so that the life expectation of the flies that emerged later was reduced.

The mean life-spans of the two sexes are based on the entire data and must not be compared directly, as their values depend on the proportions of flies from each part of the emergence range considered. The values given by the regression lines for the same dates give the best available comparison.

Efficiency of searching.

The ratio $\frac{\text{Number of flies seen}}{\text{Number known to be alive}}$ gives some measure of the efficiency of searching on each day. The denominator is found by adding the number of flies seen on the day in question to the total number of additional ones seen subsequently and it will always give a low estimate of the true population because some individuals remain undetected. It follows, therefore, that the estimated efficiency of searching is always higher than the true value.

In 1957, there was considerable day-to-day variation in the searching efficiency, and although there were signs that these differences were connected with changes in weather, analysis was impracticable because the technique had not been standardized sufficiently. The mean estimated efficiency (a) with normal searching (*i.e.*, flies not caught, wheat beaten, two workers) was 73 per cent., (b) on 'test' days (flies actually caught) was 79 per cent. and (c) when only one worker took part was 66 per cent. The efficiency also increased greatly as the season progressed, probably because practice sharpened observation.

In 1958, the technique was standardized by the time about 200 flies had been established in the cage and, on 32 occasions between 4th July and 5th August,

a standard search was made through a population consisting of at least 50 flies of each sex. The mean efficiency (males 34%, females 36%) was much lower than in 1957, but variations from varying technique were eliminated and there was no seasonal trend. Daily searching efficiencies were essentially similar for both sexes.

There was no exceptional weather during this period. The mean temperature during the observational sessions varied between 15° and 24°C. and there was no prolonged heavy rain. On some days there were showers or drizzle but these were insufficient to affect the searching efficiency.

Flies were more difficult to find on windy days than on calm ones, and on bright days than on dull ones. As the data were limited it was clearly unprofitable to attempt too fine a distinction between types of weather noted during the searching period so it was decided to consider only more windy, or less windy, occasions with 5 m.p.h. as an upper limit for the latter, and mainly sunny or mainly dull (*i.e.*, less than or more than 50% cloud cover) assigned to one of the cells of a $2 \times 2 \times 2$ classification (summarised in Table VI.)

TABLE VI.

Mean percentage efficiencies, with standard errors, according to weather and sex of flies.

	Dull		Sunny		
	More wind	Less wind	More wind	Less wind	
Males	37.7	42.4	28.0	29.9	(± 1.8) 34.3
Females	35.7	43.6	31.5	34.3	36.6
	36.7	43.0	28.7	32.1	35.3 (± 1.1)

Analysis of variance gave:—

Source of variation	d.f.	Mean Square	Variance ratio
Sun	1	1310	23.7***
Wind	1	286	5.2*
Sex	1	64	1.2
Sun \times Wind	1	56	1.0
Sun \times Sex	1	73	1.3
Wind \times Sex	1	15	
Wind \times Sun \times Sex	1	7	
Within Sub-classes	56	55.2	
	63		

* $P < 0.05$

*** $P < 0.001$

The effects of sun and wind are both significant. Although there is no statistically significant interaction, the biological meaning of the differences shown in Table VI is interesting. On dull days, male and female flies were equally easy to find and this was true irrespective of their tending to become less visible during stronger winds. On sunny days, each sex was more concealed than on dull days, both on more windy and less windy occasions, but the differences were much greater with the males and it is this that accounts for the whole difference between the percentages of males and females found. Apparently, because the

flies avoid the sun, they have little need to seek further protection from the wind. In neither sex was the difference due to wind significant on sunny days and in the males the difference was negligible. The absence of males, more obvious when conditions are seemingly adverse, is consistent with their smaller size and apparently greater fragility.

Accuracy of observations on life-span.

Dead flies were quickly destroyed by scavengers and those found could be assumed to have died within the preceding 24 hours. Usually, however, bodies were not found and with such individuals length of life was measurable only up to the last observation. Clearly it is important to try to assess the life expectation of a fly after it has been seen for the last time.

If every fly were seen every day then a reasonable expectation of life after a fly was seen for the last time would be half a day, or if every fly were seen every alternate day it would be reasonable to add half this interval, *i.e.*, one day, to the measured life-span of the flies. An estimate of this unmeasurable part of the life-span can be obtained from the original data, a small section of which is shown in Table VII. Records of the occurrence of each fly (indicated by X)

TABLE VII.

Extract from daily records.

Fly No.	Date																			
	July										August									
	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8
192	X	0	0	0	X	X	0	0	0	X	X	0	0	X	0	X	0	0	0	0
193	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	0	0
194	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
195	X	0	0	0	0	0	0	0	X	0	0	X	X	0	X	X	0	0	0	X
196	X	0	0	0	0	0	X	0	X	0	0	0	0	0	0	0	0	0	0	0

X = fly seen; X = fly last seen; 0 = fly not seen.

are separated by gaps of varying length (each day in which is indicated by 0) during which it was not seen. The accumulated frequency distribution of gaps of all lengths for all the data in fig. 6 (based on 1,744 and 2,343 gaps for males and females, respectively) shows that those of short duration were most frequent and that longer ones were progressively less frequent; thus, about 40 per cent. of all gaps were of only one day's duration, 60 per cent. of them were not more than two days long and only 3 per cent. exceeded 10 days. The blank records after the flies were seen for the last time may also be regarded as gaps which differ from the preceding ones only in that the flies failed to reappear, and it seemed likely that these gaps would have a similar frequency distribution, *i.e.*, that 40, 60, . . . 97 per cent. of them would have been of not more than 1, 2, . . . 10 days' duration had the flies reappeared. However, the flies did not

reappear and so it may be supposed that the expected intervals till death, namely, $\frac{1}{2}$, 1, . . . 5 days, followed the same distribution. The mean values for the gaps occurring within the observed life-spans of the flies were 3.05 days for males and 2.82 days for females, so that the unrecordable expectation of life was 1.5 days and 1.4 days, respectively. This method gives a useful approximation on the assumption that gaps of varying length are distributed randomly throughout the data.

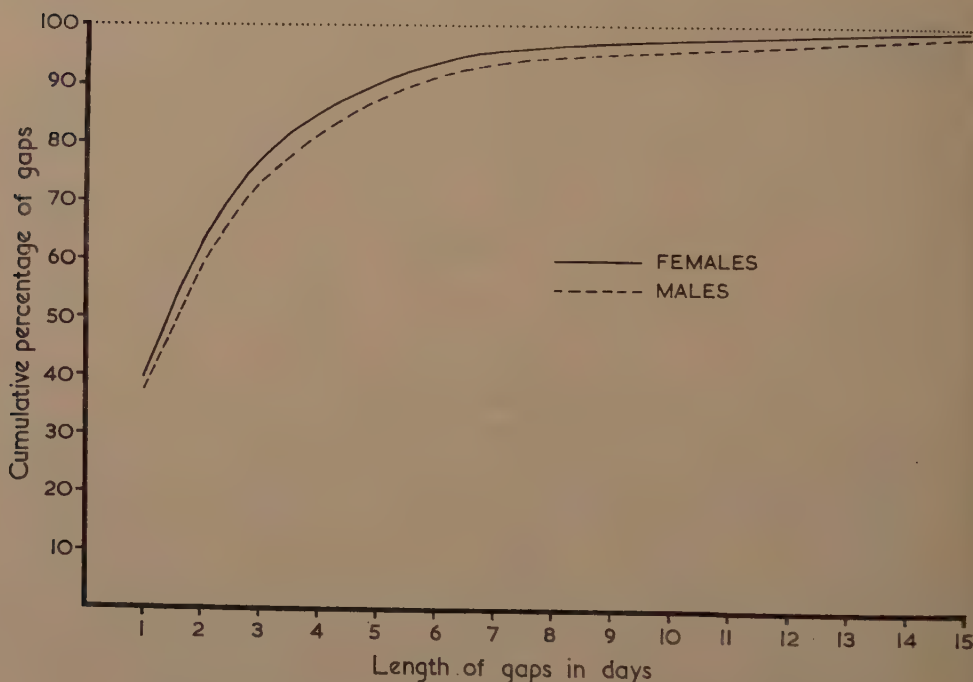


Fig. 6.—Accumulated frequency distribution of gap length in 1958 data.

If p , the probability that any particular fly will be seen on any one day, was, disregarding weather effects, constant, its true value is

$$\frac{\text{Sum, for every day, of all the flies seen}}{\text{Total number of days lived by all the flies}}$$

but the denominator derived directly from the records is too low. In Table VIII, (a) represents flies marked and released on one day. Estimates of p could be made from the complete columns starting from the left representing 1st, 2nd, 3rd . . . days after the flies' release in the cage. The difficulty is to know how many individuals to include in the total where the records show no further reappearance. This is overcome in Table VIII (b), which represents the same data rearranged according to the day on which each fly was last seen. Again the columns give estimates of p . Table IX summarises data from the 1958 experiment arranged as in VIII (b). Because the behaviour of flies that die prematurely as a result of marking is not normal, observations on those living six days or less are excluded. The totals also omit newly marked flies because these would bias the positive

records. The values of the ratios suggest a trend, indicating a tendency for the flies to have become less readily seen as they aged. The regression of 'proportion seen' y , on 'interval before the last observation' x , was calculated over the range

TABLE VIII.

Scheme illustrating rearrangement of recapture data for computing Table IX.

(a)	Days after date of release (R)																								
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	.
	R	X	0	0	0	X	0	0	X	X	0	X	X	X	0	0	0	0	X	0	0	0	0	0	.
	R	0	X	X	0	X	0	0	X	X	X	0	0	0	0	X	X	X	0	X	0	0	0	0	.
	R	X	0	0	0	X	0	X	0	0	0	X	0	0	X	X	X	0	X	0	0	0	0	0	.
	R	0	0	X	X	X	X	0	0	0	0	0	0	X	0	0	X	X	0	X	X	0	0	0	.

	R	X	0	0	0	X	X	X	X	X	0	0	X	0	X	X	0	X	0	X	X	X	0	0	.

	R	X	X	0	0	0	0	X	X	0	0	0	X	0	0	X	X	X	0	X	0	0	0	0	.
	R	0	X	X	0	0	X	0	0	X	0	X	0	X	X	X	0	X	0	0	X	0	0	0	.

(b)	Days before final observation (F)																			Unre-		Recorded		days	
.	.	.	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	F	.	.	.	
			R	X	0	0	0	X	0	0	X	X	0	X	X	X	0	0	0	0	X	0	0	.	
			R	0	X	X	0	X	0	0	X	X	X	0	0	0	0	X	X	X	0	X	0	.	
			R	X	0	0	0	X	0	X	0	0	0	X	0	0	X	X	X	0	X	0	0	.	
			R	0	0	X	X	X	X	0	0	0	0	0	X	0	0	X	X	0	X	X	0	.	
			
			R	X	0	0	0	X	X	X	X	0	0	X	0	X	X	0	X	X	X	0	0	.	
			
			R	X	X	0	0	0	0	X	X	0	0	0	X	0	0	X	X	X	0	X	0	.	
			R	0	X	X	0	0	X	0	0	X	0	X	X	X	0	X	0	0	X	0	0	.	

$x=1$ to $x=12$. Substitution of $x=0$ in the regression equation $\hat{Y} - \bar{y} = b(x - \bar{x})$ gives estimates of the 'proportion seen' appropriate to Column F, that is, estimates of the mean length of the expected interval before 'reappearance'

TABLE IX.
Estimates of searching efficiency for the 12 days before final observation.

		Days before final observation												F
		12	11	10	9	8	7	6	5	4	3	2	1	
Males ..	No. seen	68	73	79	70	77	77	72	61	70	66	75	62	261
	Total	238	242	246	248	254	257	260	261	261	261	261	261	
	Proportion seen	0.286	0.302	0.321	0.282	0.303	0.300	0.277	0.234	0.268	0.253	0.287	0.238	
Females ..	No. seen	111	110	101	98	105	100	92	93	101	95	92	97	306
	Total	292	293	296	297	300	301	304	306	306	306	306	306	
	Proportion seen	0.380	0.375	0.341	0.330	0.350	0.332	0.303	0.304	0.330	0.310	0.301	0.317	

appropriate to the flies' latter days. As before, the expectation of life after the last appearance can be taken as half this interval. The results, Table X, agree with those obtained by the previous method.

TABLE X.

Estimates of mean unrecorded lives of flies and their fiducial limits obtained by exact method.

	Males	Females
Regression coefficient b with S.E. ..	0.00503 ± 0.00174 (signif. at $P = 0.05$)	0.00609 ± 0.00133 (signif. at $P = 0.01$)
\hat{Y} (for $x = 0$)	0.2465	0.2915
95% fiducial limits of \hat{Y}	0.2180 — 0.2750	0.2692 — 0.3138
95% fiducial limits of mean expected interval until reappearance ..	2.6 — 3.6 days	2.2 — 2.7 days
Probable unrecorded life of fly ..	1.3 — 1.8 days	1.1 — 1.4 days

Discussion.

The results now described are much better than those described earlier (Dobson, Stephenson & Lofty, 1958) and many of the technical problems discussed previously have now been overcome. The most important change in technique was to use individual marks rather than marks indicating date of emergence only, because this not only made flies recognisable individually but also obviated the need for handling them during recapturing.

In the 1956 experiment, the flies had to be captured for recording and, to minimise handling, marked flies were searched for only once every three days. The present method overcame this difficulty and it had the further advantage that flies could be observed in their natural positions and postures (Dobson, 1959). Individual behaviour and movements will be described in a separate paper.

Although the technique was developed to study wheat bulb fly, it is suitable for studying other insects provided that they can be marked and that their life-histories are not affected adversely by their being confined to a restricted area. Clearly, some previous knowledge of the life-history and habits of the species under study would be an advantage; for example, if a species had a pronounced diurnal rhythm of activity the worker would have to decide on the best time to make his observations.

The accuracy of the estimates of excess over observed life-span depend on efficiency of searching but it is not always necessary or desirable to aim at high efficiency. As a general rule, the shorter the life-span of the species under study, the higher the efficiency desired. Higher efficiency can be achieved by (a) careful design and maintenance of the experimental site so that all parts can be examined easily, (b) employing more labour and searching for longer periods, (c) disturbing the site so that the animals are stimulated to activity. Care should be taken in employing these measures, however. With (a) it is necessary to guard against making the site unrepresentative of field conditions and with (c) the damage inflicted on the animals by disturbance may have adverse effects on the life-span that greatly outweigh the advantages of higher efficiency.

A high proportion of female flies obviously lived long enough to reach sexual maturity and lay eggs, and a high proportion of both sexes lived for over 30 days. This was surprising, because, in the laboratory, males often seem to be much less

long-lived than females (*e.g.*, Bardner & Kenten, 1957, and the laboratory tests of marking paints reported above). Figs. 4 and 5 show that a single statement of the mean life-span of either sex for flies living under field conditions is meaningless because the range of life-span is so great and there is apparently a trend during the season.

In an experiment of this type it is practically impossible to determine whether confining the flies to the crop and preventing their dispersal are harmful. It is not possible to study directly, or measure, the biology of free-living flies; all that can be inferred is that, as far as their occurrence on the crop can indicate, the confined flies appear to behave similarly to free-living ones, that they live for considerable periods and that they reach sexual maturity and lay eggs (Dobson, Stephenson & Loft, 1958).

The natural food of the adult wheat bulb fly is not yet known, but Long (in Mellanby, 1958, p. 159) points out that flies probably need a source of food containing sugars for continued life and egg maturation, adding that such a source is not freely available in wheat fields, suggesting that the daily dispersion of flies from the crop may be due to their foraging for food. It is interesting to note that in 1958, when the plots in the cage were weeded from time to time and very few plants other than wheat and a few grasses were present, many flies in the cage were long-lived and appeared to mature normally.

Summary.

Emergence and life-span of wheat bulb fly, *Leptohylemyia coarctata* (Fall.), have been studied by the use of a field-cage-marking technique. Emergence was investigated by observing the numbers of flies emerging daily from an area of infested wheat enclosed by a cage of fine mosquito-netting, and life-span by making a daily census of marked and individually recognisable flies which had been liberated in the cage. Flies were handled only when being marked and in the later part of the work all observations were made without touching either them or the wheat.

Flies were chilled to render them comatose for marking and under certain circumstances this and the marking was harmful. Attempts were made to reduce these harmful effects.

Emergence dates varied from year to year depending on the temperatures of spring and early summer, and there were also considerable differences between the emergence dates of populations of adjacent fields in the same year. Consistently, males appeared before females.

The ratio of the number of flies seen to the number known to be alive on each day varied according to weather, flies being more difficult to find on windy days than on calm ones and on bright days than on dull ones.

The observed life-spans of both sexes varied greatly, up to a maximum of 75 days for females and 55 days for males. An exact statement of mean life-span was not possible because there was a tendency for flies emerging later in the season to be less long-lived than those emerging earlier. Most flies of both sexes lived for over 30 days.

The observed life-spans fall short of the true life-spans by amounts that depend on the proportions of living flies seen each day. Two methods are shown by which the mean unrecorded life-span can be calculated.

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References.

- BARDNER, R. & KENTEN, J. (1957). Notes on the laboratory rearing and biology of the wheat bulb fly, *Leptohylemyia coarctata* (Fall.)—*Bull. ent. Res.* **48** pp. 821–831.
- DOBSON, R. M. (1959). Preliminary observations on the behaviour of the adult wheat bulb fly, *Leptohylemyia coarctata* (Fall.) using the “field-cage-marking” technique.—*Anim. Behav.* **7** pp. 76–80.
- DOBSON, R. M., STEPHENSON, J. W. & LOFTY, J. R. (1958). A quantitative study of a population of wheat bulb fly, *Leptohylemyia coarctata* (Fall.), in the field.—*Bull. ent. Res.* **49** pp. 95–111.
- MELLANBY, K. (1958). Entomology Department.—*Rep. Rothamst. exp. Sta.* 1957 pp. 152–166.

GENERAL INDEX

A.

- aciculus*, *Dysmicoccus*.
aculeatum, *Macromischoides*.
Adalia bipunctata, 276, 277.
advena, *Ahasverus*.
Aedes (*Aëdimorphus*), species of, in Uganda, 90.
Aedes aegypti, 78, 167, 171, 386.
Aedes aegypti formosus, 167.
Aedes aegypti queenslandensis, 167.
Aedes africanus, 167.
Aedes albocephalus, 85.
Aedes alboventralis, 85.
Aedes apicoargenteus, 167.
Aedes argenteopunctatus, 160, 168.
Aedes centropunctatus, 168.
Aedes circumluteolus, 86.
Aedes cummingsi mediopunctatus, 168.
Aedes dalzieli, 168.
Aedes dentatus, 86.
Aedes domesticus, 85.
Aedes filicis, 90.
Aedes fowleri, 168.
Aedes furcifer, 169.
Aedes gibbinsi, 85.
Aedes hirsutus, 168.
Aedes ingrami, 167.
Aedes lineatopennis, 86, 159, 160, 168.
Aedes longipalpis, 167.
Aedes luteocephalus, 167.
Aedes minutus, 168.
Aedes mucidus, 85, 167.
Aedes mutilus, 90.
Aedes palpalis, 168.
Aedes punctothoracis, 85.
Aedes quasiunivittatus, 86.
Aedes simpsoni, 167.
Aedes stokesi, 168.
Aedes tarsalis, 85, 168.
Aedes taylori, 169.
Aedes unilineatus, 167.
Aedes vittatus, 167.
Aëdimorphus (see *Aedes*).
Aëdomyia africana, 82, 166.
Aëdomyia furfurea, 83.
aegypti, *Aedes* (*Stegomyia*).
aenescens, *Culex trifilatus*.
Aeschynomene aspera, *Nupserha bicolor postbrunnea* on, 765.
aethiopicus, *Coccus*.
affinis, *Thecabius*.
Africa, South, acaricide-resistant strain of *Rhipicephalus evertsi* in, 755-764.
africana, *Aëdomyia*; *Ancala*; *Mansonia* (*Mansonioides*).
africanus, *Aedes* (*Stegomyia*); *Asperoseius*; *Coccus*.
Afrocoelichneumon didymatus, 288.
Agamomermis, 165.
Agrostis vulgaris, *Heterococcus pulverarius* on, in Britain, 673.
Ahasverus advena, 204, 205, 209, 210, 220.
Aircraft, insecticides applied from: against Chironomid larvae, 795; against *Nomadacris septemfasciata*, 441-460.
alazon, *Dysmicoccus*.
albiclavus, *Syntomosphyrum*.
alboabdominalis, *Uranotaenia*.
albocephalus, *Aedes* (*Aëdimorphus*).
alboventralis, *Aedes* (*Aëdimorphus*).
Aleochara, 276.
Aloe, *Aspidiotus destructor* on, 230.
alpinus, *Coccus*.
Amphilius krefftii, destroying Simuliid larvae, 99.
Amphorophora rubi, 308.
Ancala africana, 554.
andersoni, *Culex*.
andreas, *Culex* (*Neoculex*).
annulata, *Uranotaenia*.
annulifera, *Mansonia*.
annulioris, *Culex*.
Annulococcus, 671.
Anopheles ardensis, 90.
Anopheles brunnipes, 164.
Anopheles christyi, 77, 78, 80.
Anopheles coustani, 79, 158, 159, 163.
Anopheles coustani ziemanni, 163.
Anopheles demeilloni, 80.
Anopheles distinctus ugandae (see *A. wellcomei*).
Anopheles flavicosta, 158, 164.
Anopheles funestus, in Nigeria, 148-165; effect of house spraying on, in Tanganyika, 243-252; in Uganda, 78, 79, 80.
Anopheles funestus confusus, 242.

- Anopheles gambiae*, in Nigeria, 148–165; in Tanganyika, 243, 245, 248, 249; in Uganda, 78, 80, 81.
Anopheles garnhami, 80.
Anopheles gibbinsi, 80.
Anopheles hancocki, 80, 164.
Anopheles hancocki brohieri, *A. theileri septentrionalis* considered a synonym of, 164 (note).
Anopheles implexus, 79; recorded in Nigeria, 162, 163.
Anopheles kingi, 77, 79.
Anopheles lesoni, 164.
Anopheles longipalpis domicolus, 164.
Anopheles maculipalpis, 81, 165.
Anopheles maculipennis, 107, 108.
Anopheles marshallii, 80.
Anopheles marshallii gibbinsi, 77, 78, 80.
Anopheles moucheti, 80, 164.
Anopheles nili, 148–163.
Anopheles pharoensis, 81, 158, 165.
Anopheles pretoriensis, 165.
Anopheles rivulorum, 79; effect of house spraying on, in Tanganyika, 246–251.
Anopheles rivulorum garnhamellus, 80.
Anopheles rufipes, 158.
Anopheles rufipes ingrami, 165.
Anopheles squamosus, 81, 158, 165.
Anopheles symesi, 79.
Anopheles theileri, 80, 158, 159, 163.
Anopheles theileri septentrionalis, 164; considered a synonym of *A. hancocki brohieri*, 164 (note).
Anopheles wellcomei, 80, 148, 149, 151, 152, 155, 156–158, 160, 161, 164.
antennatus, *Culex*.
Anthocoris nemoralis, 272, 273, 277.
Anthocoris nemorum, 272, 273, 277.
Anthores leuconotus, bionomics and control of, on coffee in Tanganyika, 279–301; parasites of, 287.
Ants, culture method for aphids associated with, 7–8.
Aphelinus asychis, 304.
Aphidius avenae, 304.
Aphidius fabarum, 312.
Aphidius matricariae, 304, 312.
Aphidius ribis, 304.
Aphids, culture method for myrmecophilous, 7, 8.
Aphis gossypii, 130.
Aphodius howitti (see *A. tasmaniae*).
Aphodius pseudotasmaniae, 650.
Aphodius tasmaniae, adult biology of, in South Australia, 643–670; synonymy of, 643 (note).
apicoargenteus, *Aedes* (*Stegomyia*).
Apis mellifera, used in tests of insect-proof doorway, 135–144.
Aprostocetus, 287.
Aracercus fasciculatus, 204, 206–211, 213, 218.
ardensis, *Anopheles* (*Myzomyia*).
argenteopunctatus, *Aedes* (*Aëdimorphus*).
articulatus, *Selenaspidus*.
Artocarpus integer, *Aspidiotus destructor* on, 230.
Asperoseius africanus, 105.
Asphodelococcus, 671.
Aspidiotiphagus lounsburyi, 231.
Aspidiotus destructor, biological control of, in Principe, 223–237.
asychis, *Aphelinus*.
athenais, *Tetrastichus* (*Galeopsomyia*).
Atherigona excisa, 117.
Aitheta, 276.
Aulacorthum circumflexum, 307, 309, 310.
Aulacorthum solani, 304, 307, 309, 310, 313, 314, 317.
aurantapex, *Culex*.
aurites, *Mansonia* (*Coquillettia*).
austeni, *Glossina*.
Australia, *Aphodius tasmaniae* in, 643–670.
avenae, *Aphidius*; *Sitobion*.
Azya trinitatis, 223.

B.

- balfouri*, *Uranotaenia*.
balteatus, *Syrphus*.
Banana, *Aspidiotus destructor* on, 230; new mealybug on, 239–241.
Baris granulipennis, life-history of, on melon in Israel, 115–122.
Beans, as food for *Dysdercus supersticiosus*, 67.
Bees, Honey (see *Apis mellifera*).
BHC, against *Busseola fusca*, 321, 324, 325, 326, 333, 334, 336, 341, 342, 343; against *Hemitarsonemus latus*, 577; against *Nomadacris septemfasciata*, 454, 455; against *Pseudothraupis wayi*, 726, 727; resistance to, in strain of *Rhipicephalus evertsi*, 756, 757, 758, 759, 762.
bicolor, *Chrysops*; *Nupserha*.
bilineata, *Uranotaenia*.
bipunctata, *Adalia*.
bitaeniorhynchus, *Culex*.
Black Sage (see *Cordia macrostachya*).
Blattella germanica, 386.
Blue-tit (see *Parus caeruleus*).

Boophilus decoloratus, acaricide resistance in, 755, 762.
Brachycaudus helichrysi, 308.
brassicæ, *Brevicoryne*; *Pieris*.
Brevicoryne brassicæ, 312.
brevipalpis, *Glossina*; *Toxorhynchites*.
brevipes, *Dysmicoccus*.
 Britain, natural enemies of aphids on lettuce in, 271-278, 303-319; *Culicoides impunctatus* in, 461-489; Diptera on cereals in, 405-414, 427-433, 803-821; *Heterococcus pulverarius* in, 673; new mealybug on imported bananas in, 241; *Phyllopertha horticola* in, 353-378.
brohieri, *Anopheles hancocki*.
brumata, *Operophtera*.
brunnipes, *Anopheles*.
Bufo africanus, 170.
bukobensis, *Pseudococcus* (see *P. hargreavesi*).
 Bulrush Millet (see *Pennisetum typhoides*).
bursarius, *Pemphigus*.
Busseola fusca, tests of insecticides against, on maize in East Africa, 321-351.

C.

Cacao, aerial dispersal of vectors of virus diseases of, in Ghana, 175-201; Mirid on, in New Guinea, 519-521; *Aspidiotus destructor* on, in Principe, 230; (Stored), pests of, in Ghana, 203-222.
calamistis, *Sesamia*.
Calandra (see *Sitophilus*).
Camellia sinensis (see Tea).
Camponotus, 196.
 Canary Islands, new mealybug on bananas in, 239-241.
Capitophorus fragaefolii (*fragariae*), 276.
Carica papaya, *Pseudaulacaspis pentagona* reared on, 231.
Carpophilus dimidiatus, 204, 205, 209, 210, 213, 220.
castaneum, *Tribolium*.
 Cattle, *Rhipicephalus evertsi* on, in South Africa, 755-764; as bait for *Glossina pallidipes*, 698, 701, 702.
cautella, *Ephestia*.
celetus, *Coccus*.
celtis, *Planococcus*.
centropunctatus, *Aedes* (*Aëdimorphus*).
Ceratoteleia, 287.
cerealella, *Sitotroga*.
 Cereals, Stored, spear for sampling, 1-5.

Ceylon, *Mansonia uniformis* in, 493;
Scotinophara lurida on rice in, 559-576.
Charips tscheki, 304.
Chilo zonellus, 330.
Chilocorus pilosus, 234, 235.
Chloris chloris (Greenfinch), 272.
Chloris pycnothrix, mealybug causing distortion of, in Nigeria, 679.
Chloropisca notata (see *Thaumatomyia*).
Chnoodes cinctipennis, 223.
chorleyi, *Culex*; *Uranotaenia*.
christyi, *Anopheles* (*Myzomyia*).
chrysogaster, *Eretmapodites*.
chrysomelinus, *Tachyporus*.
Chrysops bicolor, 108.
Chrysops distinctipennis, 554.
cinctipennis, *Chnoodes*.
cinerellus, *Culex* (*Culiciomyia*).
cinereus, *Culex* (*Culiciomyia*).
circumflexum, *Aulacorthum*.
circumluteolus, *Aedes* (*Neomelaniconion*).
citri, *Planococcus*.
 Citrus, new Coccid on, in Eritrea, 395.
Cleothera, 223.
coarctata, *Leptohylemyia*.
Coccinella septempunctata, 275, 276.
Coccinella undecimpunctata, 275, 276, 277.
coccinellæ, *Tetrastichus*.
Coccus, species of, on coffee in Africa, 389-403.
Coccus aethiopicus, 401.
Coccus africanus, 389-393; related species recorded as, 393, 401.
Coccus alpinus, sp. n., on coffee, etc., in Africa, 392, 393, 394, 395.
Coccus celatus, sp. n., on coffee in Uganda, 394, 395, 397.
Coccus consimilis, sp. n., on coffee in Uganda, 396, 397.
Coccus viridis, 395, 397-399, 401.
Coccus viridulus, sp. n., on coffee in Kenya, 399, 400, 401.
cochleariae, *Phaedon*.
 Cocoa (see Cacao).
 Coconut, *Pseudothrips wayi* on, in East Africa, 57-60, 723; biological control of *Aspidiotus destructor* on, in Principe, 223-237.
 Coconut Scale (see *Aspidiotus destructor*).
Coffea, susceptibility of species of, to *Anthores leuconotus*, 290. (See Coffee.)
coffea, *Oligonychus*.
 Coffee, Coccids on, in Africa, 389-403; *Anthores leuconotus* on, in Tanganyika, 279-301.

- Coffee Borer, White (see *Anthores leuconotus*).
Colocynthis citrullus (see Watermelon).
comstocki, *Pseudococcus*.
confusus, *Anopheles bilineatus*.
 Congo, Belgian, Coccid on coffee in, 393; *Simulium neavei* and *Onchocerca volvulus* in, 9-15.
connali, *Uranotaenia bilineata*.
conradi, *Toxorhynchites brevipalpis*.
consimilis, *Coccus*.
Coquillettidia (see *Mansonia*).
Corchorus capsularis, experiments with *Nupserha bicolor postbrunnea* and, 769-771.
Corchorus olitorius, *Nupserha bicolor postbrunnea* on, in India, 765-779.
Cordia macrostachya, biological control of, in Mauritius, 123-133.
cordiae, *Schematiza*.
 Cotton, *Hemitarsonemus latus* on, in Uganda, 577-582; seeds of, as food for *Dysdercus supersticiosus*, 61-76.
coustani, *Anopheles*.
 Cowpea (see *Vigna unguiculata*).
 Crabs (*Potamon* spp.), relation of Simuliids to, in tropical Africa, 11-14, 95, 98, 108.
Cratichneumon, 288.
Crematogaster, 196.
Crematogaster striatula, 195.
crepidis, *Monoclonus*.
cressoni, *Eurytoma*.
cristata, *Mansonia* (*Coquillettidia*).
Crotalaria juncea, *Nupserha bicolor postbrunnea* on, 765.
Crotalaria saltiana, *Nupserha bicolor postbrunnea* on, 765.
Cryptognatha nodiceps, establishment of, in Principe against *Aspidiotus destructor*, 223-237.
Cryptolestes, 204, 205, 209, 210, 211, 213, 220.
Cryptophagus, 204.
 Cucumber, *Baris granulipennis* on, in Israel, 115.
Culex andersoni, 89, 91.
Culex andreanus, 86.
Culex annulioris, 77, 88, 170.
Culex antennatus, 89, 170.
Culex aurantapex, 87.
Culex bitaeniorhynchus, 87.
Culex chorleyi, 89, 91.
Culex cinerellus, 169.
Culex cinereus, 169.
Culex decens, 89, 92, 170.
Culex duttoni, 88, 170.
Culex ethiopicus, 87, 170.
Culex grahami, 77, 90, 171.
Culex guiarti, 77, 89, 170.
Culex horridus, 169.
Culex inconspicuus, 169.
Culex ingrami, 90.
Culex insignis, 87, 169.
Culex invidiosus, 89, 92.
Culex kingianus, 86.
Culex macfieii, 169.
Culex nebulosus, 169.
Culex ninagongoensis, 77, 88, 91.
Culex perfidiosus, 170.
Culex perfuscus, 89, 170.
Culex pipiens fatigans, 88, 159, 170.
Culex pipiens pipiens, 88, 91.
Culex poicilipes, 77, 87, 159, 160, 170.
Culex quasiguiarti, 89.
Culex rubinotus, 77, 86.
Culex salisburyensis, 90.
Culex semibrunneus, 87.
Culex theileri, 88.
Culex tigripes, 77, 86, 169.
Culex toroensis macrophyllus, 89, 91.
Culex trifilatus aenescens, 89.
Culex trifoliatus, 170.
Culex univittatus, 88, 170.
Culex vansomereni elgonicus, 91.
Culex weschei, 170.
Culex wigglesworthi, 169.
Culex zombaensis, 88.
Culiciomyia (see *Culex*).
Culicoides delta, in Scotland, 468, 470.
Culicoides impunctatus, flight habits of, in Scotland, 461-489.
Culicoides nubeculosus, in Scotland, 480.
Culicoides obsoletus, in Scotland, 468, 469, 470.
Culicoides pallidicornis, in Scotland, 468, 469, 470.
Culicoides pictipennis, in Scotland, 468, 470.
Culicoides pulicaris, in Scotland, 465, 468, 469, 470, 483, 485.
Culicoides punctatus, in Scotland, 468, 469, 470.
cumminsi, *Aedes* (*Aëdimorphus*).
Cycas revoluta, *Cryptognatha* on, 234, 236.
cydoniae, *Tetrastichus*.
Cynodon dactylon, mealybugs causing distortion of, in Nigeria, 677, 678, 679.
cytopus, *Hodgesia*.

D.

- Dacus*, *Syntomosphyrum glossinae* reared on, 22.
dalzieli, *Aedes* (*Aëdimorphus*).
damnosum, *Simulium*.

DDD, against *Tanytarsus lewisi*, 791, 795, 797.
 DDT, against *Busseola fusca*, 321-345; control of *Glossina* spp. by, 253-270; against *Hemitarsonemus latus*, 577-582; against *Pseudotheraptus wayi*, 725, 726, 727; against *Simulium neavei*, 14; against *Tanytarsus lewisi*, 791, 792, 793, 795, 799; in hanging drops against *Musca domestica*, 524, 525, 528, 529; use of thermal preference in bioassay of, on *M. domestica*, 382, 383, 384, 386; experiments with strains of *Rhipicephalus evertsi* and, 756, 757, 761, 762.
debege, *Simulium*.
decens, *Culex*.
decoloratus, *Boophilus*.
 Delnav, susceptibility of strains of *Rhipicephalus evertsi* to, 758, 760, 762.
delta, *Culicoides*.
demeilloni, *Anopheles* (*Myzomyia*).
dentatus, *Aedes* (*Aëdimorphus*).
 Derrisol, against *Busseola fusca*, 323, 324, 325.
detorquens, *Technomyrmex*.
Diaeretus rapae, 312.
Dianthus, *Aspidiotus destructor* on, 230.
 Diazinon, against *Busseola fusca*, 321, 338, 339.
Diceromyia (see *Aedes*).
Dichloro-diphenyl-dichloroethane (see DDD).
didymatus, *Afrocoelichneumon*.
 Dieldrin, effect of, on species balance in *Anophelines*, 242-252; against *Anthores leuconotus*, 292; application of, from aircraft against *Nomadacris septemfasciata*, 441-460; against *Pseudotheraptus wayi*, 726, 727; resistance to, in strain of *Rhipicephalus evertsi*, 757, 758, 762.
Digitaria exilis, distortion of, by mealybugs, 679.
Dimachus, 287.
 Dimethyl Phthalate, vapour of, in insect-proof doorway, 140.
dimidiatus, *Carpophilus*.
Dinarmus, 287.
 2,3-p-Dioxane S,S-Bis(O,O-diethyl phosphorodithioate) (see Delnav).
distinctipennis, *Chrysops*.
distinctus, *Anopheles* (*Myzomyia*).
domestica, *Musca*.
domesticus, *Aedes* (*Aëdimorphus*).
domicolus, *Anopheles longipalpis*.
dominica, *Rhyzopertha*.

Doorways, design of insect-proof, 135-144.
dracaenae, *Eretmapodites*.
Drosophila melanogaster, 137, 140.
dubia, *Exoplectra*.
duttoni, *Culex*.
Dysdercus supersticiosus, effects of different foods on, 61-76.
Dysmicoccus aciculus, 241.
Dysmicoccus alazon, sp.n., on bananas, 239-241.
Dysmicoccus brevipes, 190, 197.

E.

Earias, 577.
 Egypt, *Baris granulipennis* in, 115, 116; new mealybug on imported bananas in, 241.
Elaeis guineënsis, *Aspidiotus destructor* on, 230.
elgonicus, *Culex vansomereni*.
elutella, *Ephestia*.
Endochilus plagiatus, 235.
Endochilus styx, 231, 232, 234, 235.
 Endrin, against *Busseola fusca*, 321-348.
Ephestia cautella, 204-210, 213, 214, 215, 218, 219, 220.
Ephestia elutella, 215, 219.
Eretmapodites chrysogaster, 169.
Eretmapodites dracaenae, 169.
 Eritrea, new Coccid in, 393.
Erythrina, *Pinnaspis strachani* on, 231.
ethiopicus, *Culex*.
Etorleptomyia (see *Ficalbia*).
Eupelmus, 125.
euphorbiae, *Macrosiphum*.
Eurytoma, bionomics of species of, introduced into Mauritius against *Cordia macrostachya*, 123-133.
Eurytoma cressoni, 125.
Eurytoma howardi, 123.
evertsi, *Rhipicephalus*.
excisa, *Atherigona*.
exiguus, *Pharoscymnus*.
Exochomus flavipes, 235.
Exoplectra dubia, 223.

F.

fabarum, *Aphidius*.
fasciculatus, *Araecerus*.
fatigans, *Culex pipiens*.
Ferrisiana virgata, 181, 182, 188, 190, 191, 193, 194, 197.
Ficalbia flavopicta, 166.
Ficalbia hispida, 83, 166.
Ficalbia hispida sunyaniensis, 83.
Ficalbia lacustris, 83.
Ficalbia malfeyti, 77, 84.

Ficalbia mediolineata, 84.
Ficalbia mimomyiaformis, 83, 166.
Ficalbia mimomyiaformis pincerna, 83.
Ficalbia pallida, 83.
Ficalbia perplexens, 83.
Ficalbia plumosa, 83, 166.
Ficalbia splendens, 77, 83, 166.
Ficalbia uniformis, 84.
filaginis, *Pemphigus*.
filicis, *Aedes*.
Finlaya (see *Aedes*).
flavicosta, *Anopheles*.
flavipes, *Exochomus*.
flavopicta, *Ficalbia* (*Mimomyia*).
formosus, *Aedes aegypti*.
fowleri, *Aedes* (*Aëdimorphus*).
fragaefolii, *Capitophorus*.
fragariae, *Capitophorus* (see *C. fragaefolii*); *Sitobion*.
fraseri, *Mansonia*, (*Coquillettia*).
frit, *Oscinella*.
funestus, *Anopheles* (*Myzomyia*).
furcifer, *Aedes* (*Diceromyia*).
furfurea, *Aëdomyia*.
fusca, *Busseola*.
fuscipes, *Glossina palpalis*.
fuscipleuris, *Glossina*.
fuscopennata, *Mansonia* (*Coquillettia*).

G.

gahani, *Pseudococcus*.
Galeopsomopsis (see *Tetrastichus*).
Galeopsomyia (see *Tetrastichus*).
gambiae, *Anopheles* (*Myzomyia*).
Garden Chafer (see *Phyllopertha horticola*).
garnhamellus, *Anopheles rivulorum*.
garnhami, *Anopheles* (*Myzomyia*).
germanica, *Blattella*.
Ghana, aerial dispersal of cacao mealybugs in, 175-201; pests of stored cacao in, 203-222; *Glossina* spp. in, 435-440, 639-642; sleeping sickness in, 639.
gibbinsi, *Aedes* (*Aëdimorphus*); *Anopheles marshallii*.
glabra, *Thaumatomyia*.
Glossina austeni, 590, 594.
Glossina brevipalpis, 534, 553, 554; parasite of, 18.
Glossina fuscipleuris, 553, 554, 590.
Glossina longipalpis, 435, 534.
Glossina longipennis, 45, 590, 594.
Glossina medicorum, in Ghana, 435-440.
Glossina morsitans, 45, 534, 548; studies on pupal development of, 583-598; measurement of size in,

33-37; parasites of, 17-20, 22, 23, 25-31; effect of repeated applications of insecticides against, 631-637.
Glossina morsitans submorsitans, 548; parasite of, 17-20; control of, by DDT in Nigeria, 253-270.
Glossina nigrofusca, 553.
Glossina pallidipes, 35, 584, 590, 591, 593, 595; in Southern Rhodesia, 697-704; in Uganda, 533-557; and sleeping sickness, 534, 535; feeding activity of, and its relation to trypanosome challenge, 697-704; parasite of, 17, 18, 19, 23; trapping studies on, 533-557; effect of humidity and temperature on abdominal pigmentation of, 39-46.
Glossina palpalis, 590, 591, 593, 594, 595; in Ghana, 435, 639, 641; in Liberia, 550; in Uganda, 534; and sleeping sickness, 534, 639; mat passages protecting man from, 639-641; effect of trapping on, 550; parasite of, 17-20, 22, 23.
Glossina palpalis fuscipes, 45; observations on lake-side and riverine communities of, in Kenya, 47-56.
Glossina swynnertoni, 35, 45; in Kenya, 593; in Tanganyika, 589, 705-713, 781-788; fat consumption in pupae of, 590, 591, 593, 594; changes in size and fat content of adults of, 705-713; variability of fly-round catches of, 781-788.
Glossina tachinoides, 584, 594, 595; and sleeping sickness in Ghana, 639; control of, by DDT in Nigeria, 253-270; mat passages protecting man from, 639-641.
glossinae, *Syntomophyrum*.
Gnathocerus maxillosus, 204.
gossypii, *Aphis*.
Gossypium (see Cotton).
grahami, *Culex*.
graminicola, *Heterococcus*.
granarium, *Trogoderma*.
granarius, *Sitophilus*.
granulipennis, *Baris*.
Greenfinch, 272.
gregaria, *Schistocerca*.
griseicollis, *Simulium*.
guiarti, *Culex*.
Guineacorn (see Sorghum).

H.

Haematopota spp., traps for, in Uganda, 554.
hancocki, *Anopheles* (*Myzomyia*).

hargreavesi, *Pseudococcus*.
Harpagomyia taeniarostris, 165.
Harpalus, 275.
helichrysi, *Brachycaudus*.
Hemiberlesia palmarum, 231, 234, 235, 236.
Hemisarcophaga malus, 230, 231.
Hemitarsonemus latus, control of, on cotton in Uganda, 577-582.
Herbe condé (see *Cordia macrostachya*).
Heterococcus, characters of, 671, 673.
Heterococcus graminicola, 675.
Heterococcus nigeriensis, sp.n., on sorghum in Nigeria, 671-673, 677-683; distortion caused by, 677-683.
Heterococcus nudus (see *H. pulverarius*).
Heterococcus pulverarius, on grasses in Britain, 673; characters and synonymy of, 673, 674, 675.
Heterococcus variabilis, 675.
hirsutum, *Simulium*.
hirsutus, *Aedes* (*Aëdimorphus*).
hispidus, *Ficalbia* (*Mimomyia*).
Hodgesia cyrtopus, 77, 81.
Hodgesia sanguinea, 81.
hopkinsi, *Uranotaenia*.
horrida, *Neovossia*.
horridus, *Culex* (*Neoculex*).
horticola, *Phyllopertha*.
House-fly (see *Musca domestica*).
howardi, *Eurytoma*.
howitti, *Aphodius* (see *A. tasmaniae*).
Humidity, effects of: on *Glossina pallidipes*, 39-46; on *Trogoderma parabile*, 685-696.
Hyperaspis, 223.
Hyperomyzus lactucae, 304.

I.

implexus, *Anopheles*.
impunctatus, *Culicoides*.
inconspicuus, *Culex* (*Mochthogenes*).
India, *Nupserha bicolor postbrunnea* in, 765-779; *Oligonychus coffeae* on tea in, 415-426.
ingrami, *Aedes* (*Finlaya*); *Anopheles rufipes*; *Culex*.
insidiosa, *Pentilia*.
insignis, *Culex* (*Neoculex*).
invidiosus, *Culex*.
Ischnaspis longirostris, 235.
Isodrin, against *Busseola fusca*, 321, 325, 326, 327, 328, 329.
Israel, *Baris granulipennis* in, 115-122.

J.

Jack-fruit (see *Artocarpus integer*).
Jordan, *Baris granulipennis* possibly occurring in, 116.
Jute (see *Corchorus* spp.).

K.

Kenya Colony, *Pseudotheraptus wayi* on coconut in, 723; Coccids on coffee in, 393, 399, 401; *Glossina* spp. in, 47-56, 593; parasite of *G. pallidipes* in, 17-20, 23; Simuliids in, 106.
kenyae, *Planococcus*.
Khapra Beetle (see *Trogoderma granarium*).
kingi, *Anopheles* (*Myzomyia*).
kingianus, *Culex* (*Neoculex*).

L.

Lachnastoma khasiana, *Anthores leuconotus* on, in Tanganyika, 290.
lactucae, *Hyperomyzus*.
lacustris, *Ficalbia* (*Mimomyia*).
laensis, *Pseudodoniella*.
Laingiococcus, 671.
Lapsana communis, aphid on, 275.
Lasioderma serricorne, 204-210, 213, 214, 218, 219.
Lasiococcus, 231.
latus, *Hemitarsonemus*.
Lecanium (see *Coccus*).
leesoni, *Anopheles*.
Lepidosaphes, 235.
Leptohylemyia coarctata (Wheat Bulb Fly), bionomics of, in Britain, 405-414, 803-821.
Lettuce, natural enemies of aphids on, in Britain, 271-278; 303-319.
Lettuce Root Aphid (see *Pemphigus bursarius*).
leuconotus, *Anthores*.
lewisi, *Tanytarsus*.
Liberia, *Glossina palpalis* in, 550; parasite of *G. palpalis* in, 23.
Lindingaspis opimus, 230.
lineatopennis, *Aedes* (*Neomelaniconion*).
Lizards, affecting distribution of *Pseudotheraptus wayi*, 57 (note).
Locust, Desert (see *Schistocerca gregaria*).
Locust, Red (see *Nomadacris septemfasciata*).
longipalpis, *Aedes* (*Finlaya*); *Anopheles*; *Glossina*.
longipennis, *Glossina*.

longirostris, *Ischnaspis*.
Lophocateres pusillus, in stored rice,
 600, 601, 603.
lounsburyi, *Aspidiotiphagus*.
loutetense, *Simulium*.
Lucilia sericata, *Syntomosphyrum*
 spp. reared on, 17, 25.
lurida, *Scotinophara*.
luteocephalus, *Aedes* (*Stegomyia*).
Lutzia (see *Culex*).
Lygus vosseleri, 577.

M.

macfieii, *Culex* (*Culiciomyia*).
Macromischoides, 196.
Macromischoides aculeatum, new
 Coccid associated with, on coffee in
 Uganda, 397.
macrophyllus, *Culex toroensis*.
Macrosiphum euphorbiae, 304, 307,
 309, 310, 313, 314, 317.
maculipalpis, *Anopheles* (*Myzomyia*).
maculipennis, *Anopheles*; *Mansonia*
 (*Coquillettidia*); *Plutella*.
 Maize Stalk Borer (see *Busseola*
fusca).
 Maize, *Oscinella frit* on, in Britain,
 427-433; mealybugs causing distor-
 tion of, in Nigeria, 677, 679;
Busseola fusca on, in Tanganyika,
 321-351; seeds of, as food for
Dysdercus supersticiosus, 67.
 Malathion, against *Busseola fusca*,
 321, 338, 339, 343, 344; against
Pseudotheraptus wayi, 725, 726,
 727.
 Malaya, *Mansonia uniformis* in, 493.
malfeyti, *Ficalbia*.
malus, *Hemisarcopetes*.
Mansonia, 78.
Mansonia africana, 77, 85, 159, 160,
 167; distribution of, 492; biology
 of, 491-517.
Mansonia annulifera, 499, 511.
Mansonia aurites, 84.
Mansonia cristata, 84, 159, 166.
Mansonia fraseri, 85.
Mansonia fuscopennata, 84, 107.
Mansonia maculipennis, 166.
Mansonia metallica, 84.
Mansonia microannulata, 84.
Mansonia perturbans, 504.
Mansonia richardii, 505, 508.
Mansonia uniformis, 85, 159, 160,
 167; distribution of, 492; biology
 of, 491-517.
Mansonia versicolor, 84.
Mansonioides (see *Mansonia*).
marshallii, *Anopheles* (*Myzomyia*).

mashonaensis, *Uranotaenia*.
matricariae, *Aphidius*.
mauritanicus, *Tenebroides*.
 Mauritius, insects established in,
 against *Cordia macrostachya*, 123-
 133.
maxillosus, *Gnathocerus*.
medicorum, *Glossina*.
mediolineata, *Ficalbia* (*Etorleptio-*
myia).
mediopunctatus, *Aedes* (*Aedimorphus*)
cumminsi.
melanogaster, *Drosophila*.
Melanostoma mellinum, 276.
mellifera, *Apis*.
mellinum, *Melanostoma*.
 Melons, *Baris granulipennis* on, in
 Israel, 115.
metallica, *Mansonia* (*Coquillettidia*).
metallicum, *Simulium*.
Metarrhizium anisopliae, 573.
 1-Methylnaphthalene, in hanging
 drops against *Musca domestica*,
 524, 525, 528, 529, 530.
microannulata, *Mansonia* (*Coquillet-*
tidia).
 Millet, Bulrush (see *Pennisetum*
typhoides).
Mimomyia (see *Ficalbia*).
mimoyiaformis, *Ficalbia* (*Mimoyia*).
minutus, *Aedes* (*Aedimorphus*).
Mochthogenes (see *Culex*).
molitor, *Tenebrio*.
Monoctonus crepidis, 303.
Monoctonus paludum, bionomics of,
 303-319.
morsitans, *Glossina*.
 Mosquitos, swamp-breeding species of,
 in Uganda, 77-94; of Zaria Pro-
 vince (Nigeria), 145-171. (See also
Aedes, *Mansonia*, and *Anopheles*.)
moucheti, *Anopheles* (*Myzomyia*).
Mucidus (see *Aedes*).
mucidus, *Aedes* (*Mucidus*).
Musca domestica, toxicity to, of
 insecticides in hanging drops, 523-
 532; apparatus and technique for
 topical application of insecticides
 to, 715-721; use of thermal prefer-
 ence in bioassay of insecticide films
 on, 379-387; used in tests of insect-
 proof doorway, 135-144.
mutilus, *Aedes*.
Myzomyia (see *Anopheles*).
Myzus persicae, 304, 307, 309, 310,
 313.

N.

Nacoleia octasema, 173.
nacoleiae, *Pentalitomastix* (*Pseudo-*
litomastix).

Nadia ruficeps, 288.

1-Naphthyl N-Methylcarbamate (see Sevin).

Nasonovia ribis-nigri, natural enemies of, on lettuce in Britain, 275, 303-319.

naevei, *Simulium*.

nebulosus, *Culex* (*Culiciomyia*).

Necrobia rufipes, 204.

nemoralis, *Anthocoris*.

nemorum, *Anthocoris*.

Neocide M25, 14.

Neoculex (see *Culex*).

Neomelaniconion (see *Aedes*).

Neocatolaccus, 125.

Neovossia horrida, 609 (note).

New Guinea, Mirid on cacao in, 519-521.

Nigeria, new Coccid on sorghum in, 671-673, 677-683; *Glossina* spp. in, 252-270; parasite of *Glossina* spp. in, 17-20, 23; (Zaria Province), mosquitos of, 145-171.

nigeriensis, *Heterococcus*.

nigrofusca, *Glossina*.

nili, *Anopheles*.

ninagongoensis, *Culex*.

njalensis, *Pseudococcus*.

nodiceps, *Cryptognatha*.

Nomadacris septemfasciata, aircraft application of dieldrin against, in Tanganyika, 441-460; BHC against hoppers of, 454-455.

notata, *Thaumatomyia* (*Chloropisca*).

nubeculosus, *Culicoides*.

nudus, *Heterococcus* (*Phenacoccus*) (see *H. pulverarius*).

Nupserha bicolor postbrunnea, bionomics of, on jute, etc., in India, 765-779.

Nyasaland, parasites of *Glossina morsitans* in, 17-20, 22, 23; Simuliids in, 106.

nyasalandicum, *Simulium*.

O.

obsoletus, *Culicoides*.

obtusus, *Trechus*.

octasema, *Nacoleia*.

Oecophylla, associated with *Pseudococcus njalensis*, 196; affecting distribution of *Pseudothraupis wayi*, 57 (note).

Oil Palm (see *Elaeis guineensis*).

Oils, toxicity to *Musca domestica* of insecticides in hanging drops of, 523-532.

Oligonychus coffeae, on tea in India, 415-426.

Onchocerca volvulus, and Simuliids, 9, 10, 14, 95, 98, 104, 105.

O, O-Diethyl S-Ethylthiomethyl Phosphorodithioate (see Thimet).

Operophtera brumata, 271.

opimus, *Lindingaspis*.

Orculus, 231, 232, 235.

ornata, *Uranotaenia*.

Oryza sativa (see Rice).

oryzae, *Piricularia*; *Sitophilus* (*Calandra*).

Oryzaephilus surinamensis, 204.

Oscinella frit, Thimet against, on sweet corn, in England, 427-433.

Oxytelus rugosus, 276.

P.

Pachyneuron, hyperparasite of *Pemphigus bursarius*, 271.

pallida, *Ficalbia* (*Mimomyia*).

pallidicornis, *Culicoides*.

pallidipes, *Glossina*.

pallidocephala, *Uranotaenia*.

palmae, *Hemiberlesia*.

Palorus subdepressus, 204.

palpalis, *Aedes* (*Neomelaniconion*); *Glossina*.

paludum, *Monoctonus*.

papatasi, *Phlebotomus*.

Papua (see New Guinea).

parabile, *Trogoderma*.

Parus caeruleus, 272.

Pawpaw (see *Carica papaya*).

Pemphigus bursarius, natural enemies of, on poplar and lettuce in England, 271-278.

Pemphigus filaginis, 272.

Pemphigus protospirae, 272.

Penicillium citrinum, 573.

Pennisetum typhoides, mealybug causing distortion of, in Nigeria, 679; seeds of, as food for *Dysdercus supersticiosus*, 66, 67.

pentagona, *Pseudaulacaspis*.

Pentalitomastix, n.n., for *Pseudolito-*
mastix Eady, 173.

Pentalitomastix nacoleiae, 173.

Pentilia insidiosa, 223.

perfidiosus, *Culex*.

perfusus, *Culex*.

perplexens, *Ficalbia* (*Mimomyia*).

persicae, *Myzus*.

perturbans, *Mansonina*.

Phaedon cochleariae, 386.

pharoensis, *Anopheles* (*Myzomyia*).

Pharoscyrnus exiguus, 235.

Phaseolus (see Beans).

Pheidole, 196.

Phenacoccus nudus (see *Heterococcus pulverarius*).

Phlebotomus papatasi, 107, 108.

Phyllopertha horticola, bionomics and ecology of, in Britain, 353-378.

pictipennis, *Culicoides*.
Pieris brassicae, 386.
pilosus, *Chilocorus*.
pincerna, *Ficalbia* (*Mimomyia*) *mimomyiaformis*.
Pinnaspis strachani, 231.
pipiens, *Culex*.
Pipiza, 272.
Piricularia oryzae, 569, 571.
poephaga, *Sesamia*.
poecilipes, *Culex*.
Poplar, *Pemphigus bursarius* on, in England, 271-275.
Potamon (see Crabs).
plagiatus, *Endochilus*.
Planococcus celtis, 183, 197.
Planococcus citri, 181, 182, 188, 190, 191, 193, 194, 197, 199.
Planococcus kenya, 188, 190, 197.
plumosa, *Ficalbia* (*Mimomyia*).
Plutella maculipennis, 386.
pretoriensis, *Anopheles*.
Principe, biological control of *Aspidiotus destructor* in, 223-237.
Prodilis, 223.
protospirae, *Pemphigus*.
Pseudaulacaspis pentagona, 231, 234, 236.
Pseudococcus bukobensis (see *P. hargreavesi*).
Pseudococcus comstocki, 183, 188, 197; *Dysmicoccus alazon* misidentified as, 239, 241.
Pseudococcus gahani, 181, 182.
Pseudococcus hargreavesi, 188, 197.
Pseudococcus njalensis, aerial dispersal of, in Ghana, 175-201.
Pseudodoniella laensis, on cacao in New Guinea, 519; synonymy of, 519-521.
Pseudodoniella szentivanyi (see *P. laensis*).
Pseudolitomastix Eady nec Risbec (see *Pentalitomastix*).
pseudotasmaniae, *Aphodius*.
Pseudothoraptus wayi, on coconut in East Africa, 57-60, 723; factors affecting availability of, 57-60; mass rearing of, 723, 724; tests of insecticides against, 724-727.
Pterostichus, 275.
pulicaris, *Culicoides*.
pulverarius, *Heterococcus* (*Ripersia*).
punctatus, *Culicoides pulicaris*.
punctothoracis, *Aedes* (*Aëdimorphus*).
pusillus, *Lophocateres*.
Pyrethrum (*Pyrethrins*), against pests of stored cocoa, 219, 220; against *Pseudothoraptus wayi*, 725, 726, 727; in hanging drops against *Musca domestica*, 524, 527, 528.

Q.

quadristriatus, *Trechus*.
quadrivittatum, *Simulium*.
quasiguiarti, *Culex*.
quasiunivittatus, *Aedes* (*Aëdimorphus*).
queenslandensis, *Aedes aegypti*.

R.

Rainfall, effect of, on *Aphodius tasmaniae*, 643-670.
rapae, *Diaeretus*.
Rhipicephalus evertsi, acaricide-resistant strain of, in South Africa, 755-764.
Rhodesia, Northern, parasite of *Glossina morsitans* in, 23.
Rhodesia, Southern, *Glossina pallidipes* in, 697-704.
Rhothane, 795 (note).
Rhyzopertha dominica, in stored rice, 599-630.
ribis, *Aphidius*.
ribis-nigri, *Nasonovia*.
Rice (*Oryza sativa*), *Scotinophara lurida* on, in Ceylon, 559-576; distortion of, by mealybugs, 679; (Stored), insects infesting, 599-630.
richardii, *Mansonia* (*Coquillettidia*).
Ripersia pulveraria (see *Heterococcus*).
rivulorum, *Anopheles* (*Myzomyia*).
rubi, *Amphorophora*.
rubinotus, *Culex* (*Neoculex*).
ruficeps, *Nadia*.
rufipes, *Anopheles*; *Necrobia*; *Tachinus*.
rugosus, *Oxytelus*.

S.

salisburyensis, *Culex* (*Neoculex*).
sanguinea, *Hodgesia*.
São Tomé, Coccids and predators on coconut in, 235.
sasakii, *Sitophilus*.
Schematiza cordiae, establishment of, in Mauritius, 123-133.
Schistocerca gregaria, group effects on feeding and maturation of males of, 731-753.
Scotinophara lurida, bionomics of, on rice in Ceylon, 559-576.
Selenaspidus articulatus, 235.
semibrunneus, *Culex* (*Culiciomyia*).
septemfasciata, *Nomadacris*.
septempunctata, *Coccinella*.
septentrionalis, *Anopheles theileri*.
sericata, *Lucilia*.

serricorne, *Lasioderma*.
Sesamia calamistis, 330.
Sesamia poephaga, 330.
Sesbania, *Nupserha bicolor* post-brunnea on, 765, 766, 767, 768, 769.
 Sevin, susceptibility of strains of *Rhipicephalus evertsi* to, 759, 761, 762.
simpsoni, *Aedes* (*Stegomyia*).
Simulium damnosum, 95, 98, 99, 101, 103, 104, 105, 109.
Simulium debegene, 96, 109.
Simulium griseicollae, 96.
Simulium hirsutum, 96.
Simulium loutetense, 98.
Simulium metallicum, 101.
Simulium neavei, and *Onchocerca volvulus* in Belgian Congo, 9-15; observations on members of complex of, in Tanganyika, 95-113.
Simulium nyasalandicum, 106.
Simulium quadrivittatum, 101.
Simulium unicornutum, 96.
Simulium vorax, 96.
Simulium woodi, 106.
Sitobion avenae, 308.
Sitobion fragariae, 308.
Sitophilus granarius, 615.
Sitophilus (*Calandra*) *oryzae*, 204, 600, 625.
Sitophilus sasakii, in stored rice, 599-630.
Sitotroga cerealella, in stored rice, 599, 600, 601, 603, 606, 609, 610, 615.
 Sleeping Sickness, in Ghana, 639; in Uganda, 534, 535, 553; and *Glossina* spp., 534, 535, 553, 639.
 Sodium Arsenite, susceptibility to, in strains of *Rhipicephalus evertsi*, 756, 757, 758, 760, 762.
solani, *Aulacorthum*.
Sonchus asper, aphid on, 275.
 Sorghum, finding and effects of new Coccid on, in Nigeria, 671-673, 677-683; seeds of, as food for *Dysdercus supersticiosus*, 61-76.
 Spear, for sampling bulk grain, 1-5.
Spilochalcis, 125.
splendens, *Ficalbia* (*Mimomyia*).
Spodoptera, on maize in Tanganyika, 339, 341, 344.
squamosus, *Anopheles* (*Myzomyia*).
Stegomyia (see *Aedes*).
stellifera, *Vinsonia*.
stokesi, *Aedes* (*Aëdimorphus*).
strachani, *Pinnaspis*.
striatula, *Crematogaster*.
styx, *Endochilus*.
subdepressus, *Palorus*.
submorsitans, *Glossina morsitans*.

Sudan, *Tanytarsus lewisi* in, 789-801.
sunyaniensis, *Ficalbia* (*Mimomyia*) *hispida*.
supersticiosus, *Dysdercus*.
surinamensis, *Oryzaephilus*.
 Sweet Corn (see Maize).
swynnertoni, *Glossina*.
symesi, *Anopheles*.
Syntomaspis (see *Torymus*).
Syntomosphyrum, studies on species of, parasitic on *Glossina* spp., 17-20, 21-23, 25-31.
Syntomosphyrum albiclavus, sp.n., 22-31.
Syntomosphyrum glossinae, 17-20, 21-23, 25-31.
Syrphus balteatus, 272, 275.
szentivanyi, *Pseudodoniella* (see *P. laensis*).

T.

Tabanus spp., traps for, in Uganda, 554.
tachinoides, *Glossina*.
Tachinus rufipes, 276.
Tachyporus chrysomelinus, 276.
taeniarostris, *Harpagomyia*.
 Tanganyika Territory, *Pseudotharaptus wayi* on coconut in, 723; pests of coffee in, 279-301, 399; *Busseola fusca* on maize in, 321-351; *Nomadacris septemfasciata* in, 441-460; *Glossina* spp. in, 39-46, 705-713, 781-788; parasites of *G. morsitans* in, 17-20, 22, 23, 25; mosquitos in, 242-252, 493; Simuliids and onchocerciasis in, 95-113.
Tanytarsus lewisi, bionomics and control of, in Sudan, 789-801.
tarsalis, *Aedes* (*Aëdimorphus*).
tasmaniae, *Aphodius*.
taylori, *Aedes* (*Diceromyia*).
 Tea, *Oligonychus coffeae* on, in India, 415-426.
Technomyrmex detorquens, 130.
Telenomus triptus, 573, 574.
 Temperature, effects of: on *Glossina* spp., 39-46, 583-598; on *Trogoderma parabile*, 685-696.
Tenebrio molitor, 386.
Tenebroides mauritanicus, 204.
Tetrastichus, 125, 287.
Tetrastichus athenais, 125.
Tetrastichus coccinellae, 234.
Tetrastichus cydoniae, 234.
Tetrastichus valerus, 125.
Thaumatomyia glabra, 137, 140, 275.
Thaumatomyia notata, 275.
Thecabius affinis, 272.

- theileri*, *Anopheles* (Myzomyia); *Culex*.
 Thimet, against *Oscinella frit*, 427-433.
tigripes, *Culex* (Lutzia).
toroensis, *Culex*.
Torymus, 125.
 Toxaphene, resistance to, in strain of *Rhipicephalus evertsi*, 755, 756, 757, 758, 759, 762.
Toxorhynchites brevipalpis conradti, 171.
Toxorhynchites viridibasis, 171.
 Traps, for *Glossina*, 533-557.
Trechus obtusus, 275, 276.
Trechus quadristriatus, 275.
Tribolium castaneum, 204, 205, 209, 210, 214, 220.
trifilatus, *Culex*.
 Trinidad, Coccinellids introduced into Principe from, against *Aspidiotus destructor*, 223.
trinitatis, *Azya*.
triptus, *Telenomus*.
Triticum aestivum (see Wheat).
Trogoderma granarium, 4, 685, 692, 693, 694.
Trogoderma parabile, factors affecting development and diapause in, 685-696.
Trypanosoma gambiense, in Uganda, 534.
Trypanosoma rhodesiense, vectors of, in Uganda, 534, 535, 553.
 Trypanosome Challenge, feeding activity of *Glossina pallidipes* in relation to, 701, 702.
tscheki, *Charips*.
 Tsetse Flies (see *Glossina*).

U.

- Uganda, Coccids on coffee in, 395, 397, 399; *Hemitarsonemus latus* on cotton in, 577-582; *Glossina* spp. and sleeping sickness in, 534, 535; investigations on *G. pallidipes* in, 533-557; parasite of *G. palpalis* in, 22; mosquitos in, 77-94, 493.
ugandae, *Anopheles distinctus* (see *A. wellcomei*).
undecimpunctata, *Coccinella*.
unicornutum, *Simulium*.
uniformis, *Ficalbia*; *Mansonia* (*Mansonioides*).

- unilineatus*, *Aedes* (*Stegomyia*).
univittatus, *Culex*.
Uranotaenia alboabdominalis, 82, 90.
Uranotaenia annulata, 166.
Uranotaenia balfouri, 82.
Uranotaenia bilineata connali, 165.
Uranotaenia chorleyi, 82, 166.
Uranotaenia hopkinsi, 82.
Uranotaenia mashonaensis, 82, 166.
Uranotaenia ornata, 166.
Uranotaenia pallidocephala, 77, 81.

V.

- valerus*, *Tetrastichus* (*Galeopsomopsis*).
vansomereni, *Culex*.
variabilis, *Heterococcus*.
Verania vincta, 424.
versicolor, *Mansonia* (*Coquillettidia*).
Vigna unguiculata, as food for *Dysdercus supersticiosus*, 67.
vincta, *Verania*.
Vinsonia stellifera, 235.
virgata, *Ferrisia*.
viridibasis, *Toxorhynchites*.
viridis, *Coccus*.
viridulus, *Coccus*.
vittatus, *Aedes* (*Stegomyia*).
vorax, *Simulium*.
vosseleri, *Lygus*.

W.

- Watermelon, *Baris granulipennis* on, in Israel, 115.
wayi, *Pseudothertaptus*.
wellcomei, *Anopheles* (*Myzomyia*).
weschei, *Culex*.
 Wheat (*Triticum aestivum*), *Leptohylemyia coarctata* on, in Britain, 405-414, 803-821; distortion of, by mealybugs, 679.
 Wheat Bulb Fly (see *Leptohylemyia coarctata*).
wigglesworthi, *Culex* (*Neoculex*).
woodi, *Simulium*.
Wuchereria bancrofti, 98.

Z.

- Zanzibar, *Pseudothertaptus wayi* on coconut in, 57-60, 723.
Zea mays (see Maize).
ziemanni, *Anopheles coustani*.
zombaensis, *Culex*.
zonellus, *Chilo*.

INDEX TO AUTHORS

Baker, J. A. F., 755.
 Bedford, H. W., 789.
 Blasdale, P., 253, 265.
 Breese, M. H., 599.
 Brown, A. W. A., 789.
 Browne, S. G., 9.
 Burges, H. D., 1, 685.
 Bursell, E., 33, 39, 47, 583, 705.

Chapman, R. F., 435.
 Coaker, T. H., 61.
 Cornwell, P. B., 175.
 Cranham, J. E., 203.
 Croix, E. A. S., La, 639.

Das, G. M., 415.
 Davies, H., 265.
 De Lotto G., 389.
 Dobson, R. M., 803.
 Dun, J. A., 271.
 Dutt, N., 765.

Eady, R. D., 173.

Fernando, H. E., 559.

Geering, Q. A., 61.
 Gillham, E. M., 379.
 Gillies, M. T., 243.
 Glasgow, J. P., 47, 705, 781.
 Goma, L. K. H., 77.
 Gostick, K. G., 523.
 Griffiths, D. C., 303.

Hanney, P. W., 145.
 Harris, E., 677.
 Hewlett, P. S., 523.
 Hocking, B., 135.

Ingram, W. R., 577.

Jepson, W. F., 427.

Kerrich, G. J., 21.
 Kettle, D. S., 461.
 Kirby, W. W., 253, 265.

La Croix, E. A. S., 639.
 Laurence, B. R., 491.
 Leggate, B. M., 697.
 Lewis, D. J., 95.
 Long, D. B., 405.
 Lotto, G. De, 389.

McKinley, D. J., 789.
 Maelzer, D. A., 643.
 Mathias, P., 427.
 Milne, A., 353.
 Morris, K. R. S., 533.
 Morris, M. G., 803.
 Muir, D. A., 7.

Norris, M. J., 731.

Odhiambo, T. R., 519.

Pilson, R. D., 697.
 Potter, C., 379.

Qutubuddin, M., 789.

Rivnay, E., 115.

Saunders, D. S., 17, 25.
 Sawicki, R. M., 715.
 Simmonds, F. J., 223.
 Simpson, H. R., 631.
 Smith, A., 243.

Tapley, R. G., 279.

Vanderplank, F. L., 57.

Walker, P. T., 321.
 Ward, J., 379.
 Wheatley, P. E., 723.
 Whitehead, G. B., 755.
 Wiehe, P. O., 132.
 Williams, D. J., 239, 671.
 Williams, J. R., 123.

Yeo, D., 631.
 Yule, W. N., 441.

